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Version: Version of Record

Link(s) to article on publisher's website:

<http://dx.doi.org/doi:10.21954/ou.ro.0000ef05>

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Foraging behaviour of king penguins
(*Aptenodytes patagonicus*) in relation to oceanography
at South Georgia and Kerguelen



A thesis submitted to the Open University
for the degree of Doctor of Philosophy
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22nd April 2013

Date of Submission: 24 April 2013
Date of Award: 7 October 2013

This thesis is based on my own work as well as on work with collaborators. The data used for this thesis have been collected by the British Antarctic Survey (Chapter 3) and the Centre d'Etudes Biologiques de Chizé (Chapters 4-6). The data of the field season 2009/10 at Kerguelen used in Chapter 5 have been collected during my own fieldwork carried out with the Centre d'Etudes Biologiques de Chizé.

Abstract

Understanding the levels of variability in oceanographic features where marine predators forage is critical for understanding variability in an animal's foraging behaviour and reproductive success, and for assessing their potential reactions to environmental change.

In this thesis, I examine the foraging behaviour of king penguins (*Aptenodytes patagonicus*) in relation to oceanographic features in both horizontal and vertical dimensions. I used ARGOS and Global Positioning System tracking data combined with Time-Depth-Temperature-Recorder data to follow the at-sea movements for penguins breeding at South Georgia and Kerguelen. Combining penguin behaviour with oceanographic data at the surface and at depth allowed me to explore how animals adjust their horizontal and vertical movements in response to their environment. In this context I investigated how horizontal habitat use may relate to different Antarctic Circumpolar Current frontal zones, and how hydrological structures at depth may impact diving behaviour.

At both study locations, the Polar Front (PF) and cold-water features of southern origin were key features used during foraging. The importance of local habitat was reflected in their use of mesoscale eddies at South Georgia, and bathymetry-related upwelling at Kerguelen. The main features used at depth, during prey pursuit, were the thermocline and Winter Water. Penguins also explored Circumpolar Deep Water, which appears to represent an important foraging niche for birds when under increased breeding or environmental constraints. Variability in the PF and in cold-water features in the foraging area significantly affected penguin behaviour. For example, penguins showed altered behavioural responses and low reproductive success following shifts in key oceanographic features during one breeding season.

My study of king penguin foraging behaviour in two sectors of the Southern Ocean has generated these key insights into foraging relationships with oceanography, and into penguin's adaptive capacities to environmental variability. This is of importance for assessing possible reactions of king penguins towards environmental change.

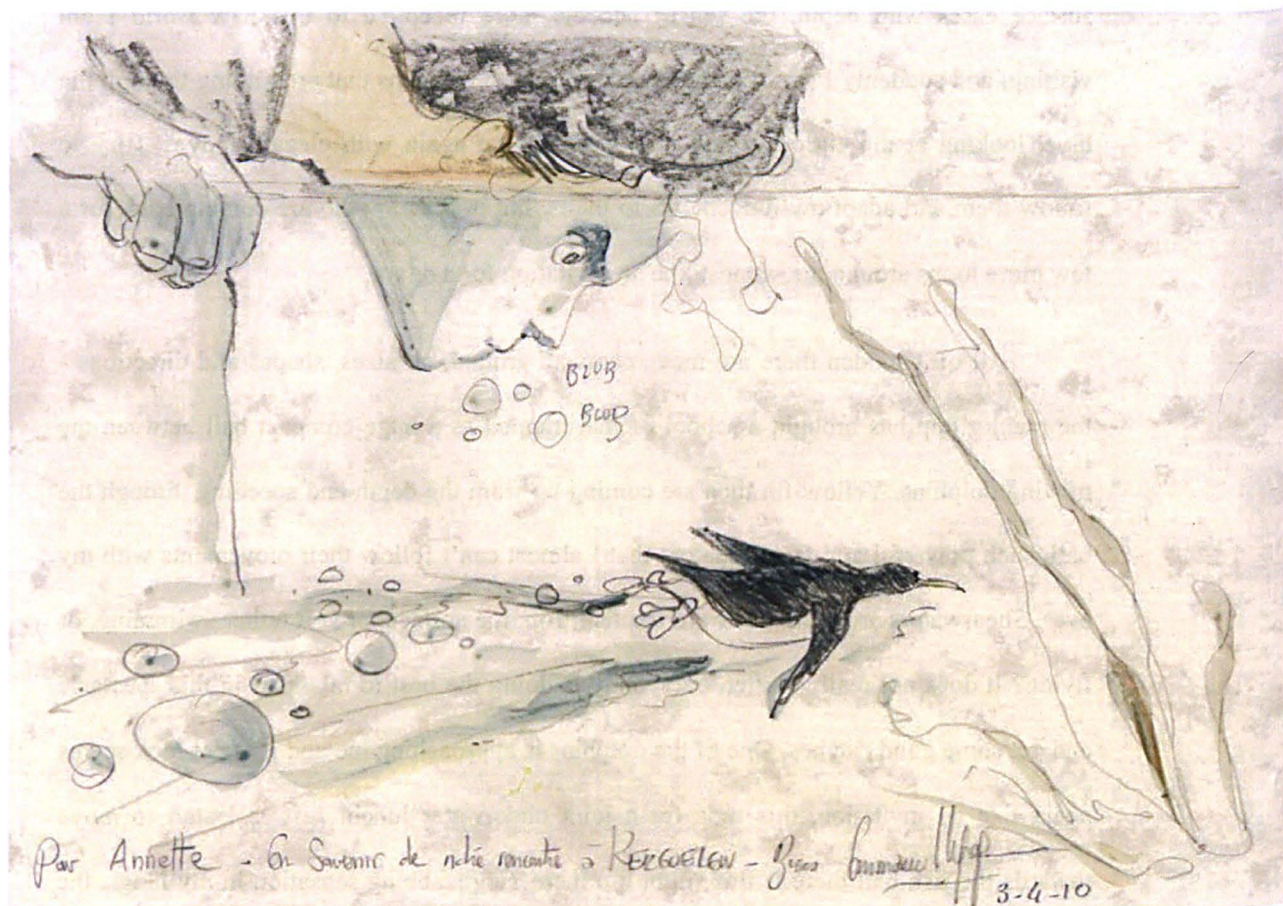
Preface

In the middle of the Atlantic Ocean, diving down into the deep blue towards the thousands of sunrays reflected from the endless blue. The world's noise stops suddenly, and time seems to become less important as I am moving deeper into the blue. I can see shadows moving underneath, still too far to reach. As the struggle to move away from the surface eases with depth, the senses become more receptive to this new world I am visiting, and suddenly I am in company of a group of dolphins that are gliding through the blue, looking at me curiously and then speeding up again with elegant moves. I try to follow them and adapt my movements to theirs, but it is them who are coming back for a few more loops around me, almost like an invitation for a dance.

All of a sudden there are movements all around, all sizes, shapes and directions - the main group has brought a school of fish trapped as a huge compact ball between the moving dolphins. Yellow-fin tuna are coming up from the depth and speeding through the ball, such powerful and fast predators that I almost can't follow their movements with my eyes. Shearwaters are gliding toward the fish from the surface, or is it rather swimming, or flying? It does not really matter, everybody is doing the best to take part in this spectacle and get some good catches. One of the dolphins is approaching me and its brief look seems again like an invitation, this time for a joint underwater lunch. Just as I start to move towards the fish ball there is this slight but increasing stabbing sensation in my lungs, the reminder that I am only a visitor in this world, and have to return to the surface. A last look on the spectacle, it is already moving away from me, as I start moving my fins upwards, frustrated once again by the sudden return to reality and my inability to stay in the blue for longer.

These experiences in the mid-Atlantic deep blue have brought me to embark on this PhD. Now I am at the end of 4 years of trying to find out how animals move in their

underwater world, how they may perceive the ocean currents and water masses, and how they may find and catch their prey. It has been an amazing journey into the world of the deep blue, and I often imagined myself diving again while sitting at the desk looking at dive profiles, this time with the kings in the ocean around South Georgia and Kerguelen.



Drawing by Emmanuel Lepage, Kerguelen in April 2010.

Acknowledgements

This PhD has been a truly amazing journey, with a flavour of a marathon towards the end, and I would not have been able to complete this work without the help and support of many people over the last 4 years.

First at all I want to thank my supervisors **Phil Trathan** and **Charly Bost** for their great guidance and support over the course of this work. There was always a perfect balance of help and guidance on one side, and freedom to realize my own ideas on the other side. Their ideas and unrestricted support had a major influence on this thesis, and have shaped me both as a scientist as well as a person. I truly hope that we can keep working together in the future. Charly, I have spent a wonderful and unforgettable time South at Crozet and Kerguelen, thank you so much for making that possible and taking me to your islands. Phil, many thanks for these great discussions ranging from science and methodological issues to the broader ecology context until any other aspect of life. I want to thank you both for your confidence and support from the start of this project, which is a fundamental part of a not regularly funded PhD.

At BAS I met many amazing people who have always given me new inspiration and motivation to try new approaches to my work, and step back to see things in a broader frame. I would like to thank all these people, even if I can't name them all, for this special and stimulating atmosphere, and for being so open to share their knowledge and answer questions. In particular I would like to thank Norm, Jaume, Richard, Janet, Ian, Mike, Damien, Ryan, Gabi, Sophie, Claire, Nadine, José for their help and advice, but also for nice chats and smiles in the corridors. I would also like to thank Hugh VENABLES for all his help with oceanography – thanks for your patience when explaining how the ocean works, and also for some nice chats about seabirds, whales and other wildlife. Will and Silvia, and Hannah and Eugene thank you for great times in BAS as well as in Cambridge life. To Jo Milton for her help concerning whatever issue of the library, and for her encouragements during some of the library days of my final writing up. To Audrey Stevens for the outreach activities planned together, I have learned a lot about talking science to kids and other people from you! And finally thanks to my officemates Elise, Cat and Tom for a fun and good mood office!

Many big thanks to **Alison Teague**, who is doing such a great job as a student coordinator at BAS. She made life so much easier by taking tasks off the students and turning problems into solutions, and always had time to listen and a smile to turn things positive. She has definitely contributed to getting this PhD done in the way it went, and it has been a great pleasure to work with her.

Now to the **Chizé** gang – unforgettable moments in this beautiful part of France in the company of you guys. My housemates Clara and Matthieu, we had such a great time in the house in Availles, gardening and getting visits from our lovely neighbours, and of course the aperitifs... Matthieu our visits to the market and philosophical breakfasts were the best start into the day! Thanks to JB Thiebot, Janos, Hélène, Aurélie, Anne-Cécile, Morgane, Deborah, Thiebot, Miches, and to Cédric, Paul, Jim and Flore for great times on the beach with surf and food. In the Chizé lab there was Yves Cherel, Henri Weimerskirch, Christophe Guinet, Christophe Barbraud, David Pinaud and Karine Delord who had always open doors for help and advice, always a smile in the corridor and great company outside of the lab life. I will never forget our lovely neighbours in Availles – Lilian, Chantale, Michel and Marie-Thérèse. They have given a very particular note to my time in Chizé, and added so much charme and quality of life, from advice on gardening over vintage to apéros with vin de noix and pineau and delicious dinners. Last but not least the family Bost who received me so heartily in Chizé and with who I had the chance to spend so many nice moments.

Concerning my **fieldwork**, I am particularly grateful to Alexis Chevallier and Pierrick Giraudet for their help with the king penguin tagging at Kerguelen. They have been great help at all times, and particularly regarding our field season in 2009/10 where they went back regularly to the remote Ratmanoff colony after I had left the island to look for lost loggers. I enjoyed very much their company during this summer on a remote island in the Southern Ocean, between Ratmanoff, Pointe Suzanne and Mayès. I have also learned a lot about seabirds during that time, thanks a lot for your teaching and your patience! Many thanks also to Léo, Lise, Clément, François, Nory, JB Pons, Jules et Poussin, Nina, Matthieu le Gener, Mouhecaca and les Poptruites, Fabrice, Domi, Philou and Audrey for all the nice moments spent together at Kerguelen, at for the friendships that have extended beyond the Southern Ocean. Thanks to Daniel for nice moments with chats about mermaids, waves trying to catch the stars and Antarctic sailors afraid of icecubes. And of course to Moustache for great times in the field, introductions into La Réunion culture and food, and hosting us so generously with his family on our return from South. There is also

the Crozet crowd that I would like to thank for their help and company, first at all the other two Charlie's Angels Astrid and Alice, Aurel and the geologists for a really nice time together in the field, Marion & Marion, Nico, Gwendal and Rémi.

In **Cambridge** there were a couple of people who have added much pleasure to my time here. Sae, my almost-sister, how can I thank you for all these nice moments, encouragements, advice and times that just took my mind off issues related to thesis writing. I am looking forward to having more spare time now to spend with you. Rocio, always there in good and bad times, always cheering me up and adding a positive flavour to life. Thank you for the fantastic weekend breakfasts, the gardening, and your friendship. I hope for more shared adventures to come in the future! Thanks to the Tango guys for keeping up my sanity with dancing, Annette, Savio, Angel, Elwina and particularly Christian for the Cambridge Underground Tango teaching! Sebastian and Carla, that was a great couple of months that we have spent together, thanks for bringing some fresh latino wind and for all our nice moments. I seriously hope to see you again between Europe and Uruguay. Peter it was a very pleasant surprise to meet you here in Cambridge and to share 3 years with you!

During my PhD I spent some time in the **Azores** where I have made so many amazing experiences and met so many remarkable people. I would like to thank Fernando to take me just in the middle of foraging tuna, one of the most amazing things I have ever seen. Leonildo and Emanuel for finding the best spots to observe the animals, and for teaching me so many things about the ocean that I could not have learned from books. Edouardo for his advice on all aspects of Azorean life, and his sincere friendship over the course of all the years. Thanks to Norberto Serpa and his crew, to Foca, Frank, Souzanna, Takoni and all the Horta people. My thanks also go to Monica Silva, Claudia and Irma from DOP for keeping my scientific view on things alive. To Enrico and Dania, Michael and Justin, Lisa, Gilberto, Faith, David and all the others that I have met there. To Karin Hartman for great times on land and on the ocean, at the surface and under water. Finally I would like to thank Frank Wirth for being all at the start of my Azorean journey, which has finally brought me to the point where I am now.

To some special people that have accompanied me since **Marseille** and given me energy throughout this PhD, even though now dispersed in different parts of the world. Kim, Angela, Valentine, Adrien, Soledad, Anna, Etienne, JB, Celia, Nono, you were great mental company during the PhD and I will try my best to turn it into real company again very soon.

A couple of people back in **Germany** that keep in touch even though I have spend extended periods away – Estelle, Simon, Sven, all the kajaking gang, Timo, and also the almost-family members Nines, Stefan and Julieta in Landau.

Finally I want to thank my family, particularly my parents Tobias and Johanna, and my brother Wolfgang, who have supported me all the time in every way possible, encouraging me to follow my interests until the end. Lena Marie and Manuel for being such amazing kids who managed to take my mind completely off work within seconds. Lastly I want to thank Johnnie for all his support, encouragement, help and love, for putting up with time-consuming work and some bad moods particularly towards the end of this PhD. And, Johnnie you wanted to hear that – thanks for all the crisps!

I would like to dedicate this thesis to these last very special people, and particularly to my grandmother Johanna who has supported and encouraged me for as long as I can remember until almost the end of my PhD.

List of abbreviations used in this thesis:

ACC – Antarctic Circumpolar Current

PF – Polar Front; SPF – southern PF; NPF – northern PF

PFZ – Polar Frontal Zone

AAZ – Antarctic Zone

SACCF – Southern ACC Front

SB – Southern Boundary

FTC – Fawn Trough Current

SML – Surface Mixed Layer

TH – Thermocline

WW – Winter Water

CDW – Circumpolar Deep Water

UCDW – Upper CDW

mCDW – modified CDW

SST – Sea Surface Temperature (°C)

SSTA – Sea Surface Temperature Anomaly (°C)

SSH – Sea Surface Height (dynamic cm)

TDR – Time-depth-recorder

GPS – Global Positioning System

BMG – Body mass gain (kg)

FZC – Foraging Zone Coefficient

ARS – Area Restricted Search

BrIdx – Broadness Index

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Chapter 1

General Introduction



1.1 Foraging

1.1.1 Foraging ecology: link between environment, fitness and demography

Foraging is a crucial behaviour for animals, determining the quantity of energy that can be allocated to life-history traits such as survival, growth or reproduction (Boggs 1992). Resources acquired while foraging ultimately impact population development through the direct and indirect effects of individual survival and fecundity. The connection between the environment and population development is therefore probably mediated through resource acquisition and allocation (Stearns 1992). While variability in the physical environment is known to affect the availability and accessibility of resources, foragers have to find strategies to optimally explore the resources available, which in turn, ultimately determines the allocation of energy towards maintenance and reproduction. Foraging in terms of strategy and success is therefore strongly impacted by both the environment as well as the forager's strategy to explore the limited resources in a given environment.

The demands of food acquisition consequently exert strong selective forces on the anatomy, physiology, and behaviour of birds. Following evolutionary theory, natural selection should favour individuals adopting strategies that optimize the exploration of the available resources (Stearns 1992). In this context a strategy is defined as an adaptive response chosen within a range of possible solutions, where responses can be of a behavioural, physiological or morphological nature. Natural selection for efficient foraging affects decisions about prey choice, patch choice for foraging and patch exploitation strategy (Stephens & Krebs 1986). Between the varieties of strategies adopted by the individual of one species, some are more successful regarding survival, reproduction and consequently the relative contribution of the individual in terms of descendants, i.e. increasing that individual's fitness (Stevick et al. 2002). Over generations, the mechanisms of natural selection have lead to behaviours which increase the survival and reproduction

of an individual in a given environment (Darwin 1859). A population will therefore progressively evolve through selection of individuals with better adaptation to their environment. However, in this context evolution should not be seen as leading to perfectly adapted species, but rather to well adapted to the current circumstances.

Although relationships between environmental parameters and life-history traits have been increasingly documented (Weimerskirch et al. 2003; Forcada et al. 2005; Forcada et al. 2006; Jenouvrier et al. 2005; Jenouvrier et al. 2009; Barbraud & Weimerskirch 2006; Barbraud et al. 2011), understanding how such relationships develop and are maintained in a changing environment is less well understood. Investigating the foraging behaviour of animals in relation to their environment is therefore crucial to better understand the link between population development and their environmental conditions (Hughes 2000). In a changing environment, the understanding of such links becomes particularly important in the context of assessing potential reactions of animal populations towards future environmental change (Trathan et al. 2007). Under current predictions it is important to understand how marine predators explore their environment (Trathan et al. 2007; Forcada & Trathan 2009; Péron et al. 2012), and identify possible key oceanographic features targeted during foraging, to be able to understand currently observed behaviour and population development, and assess potential future changes (Parmesan 2006).

1.1.2 Optimal foraging theory and central place foragers

The selective value of differences in foraging behaviour is almost certainly directly dependent upon an individual's foraging performance in terms of energy gain from prey ingestion. **Optimal foraging theory** states that organisms forage in a way so as to maximize their net energy input per unit time (Charnov 1976; MacArthur & Pianka 1966; Stephens & Krebs 1986), and that such optimization of foraging is a selective value in evolution (MacArthur & Pianka 1966). This approach has shown that foragers do not

necessarily choose their prey dependent upon its abundance in the environment, but rather as a function of energetic optimization of time allocated to the exploration of such resources (Charnov 1976) depending upon the profitability of the prey resources in terms of patch density as well as on travel time necessary to reach it and other aspects related to prey handling time (Schoener 1979). This means that foragers move through their environment in a dynamic way, adjusting time allocation within prey patches in order to optimize foraging in terms of energy intake per unit time (Schoener 1979). Consequently species of high foraging flexibility with the possibility of behavioural adaptation have better abilities to optimize foraging and survive in a variable environment (MacArthur & Pianka 1966). Furthermore individuals with a specialized diet will be more affected by the reduction or the disappearance of their prey, whereas more generalist individuals have better capacities of adaptation to potential changes in the abundance of one prey type by switching to the exploration of other resources (Annett & Pierotti 1999).

Constraints on central place foragers

Central place foragers (Orians & Pearson 1979) represent a particular case of foragers constrained by the need for regular returns to the breeding place to provide the offspring with food. Central place foragers therefore differ from others in that their activities include an outbound journey, a period of searching, and then a return journey. Foraging decisions in central-place foragers thus concern both the travel times to the resources as well as the quantity and quality of prey (Orians & Pearson 1979; Bell 1990; Krebs & Davies 1993). Seasonal constraints on the animals may further impact the behaviour of central-place foragers, with changing time and energy budgets due to the breeding cycle leading to different foraging decisions and degrees of foraging optimization in terms of net energy gain per unit time, and therefore to changes in the exploration of prey resources. During the reproduction period, central-place foragers have to return to the colony regularly to

provide their offspring with food or to relieve their partner, this means that they may need to forage in areas close to the colony. Seasonality in their prey species will add further complexities in their optimal decisions.

During the breeding season, increasing demands and constraints on animals may increase foraging optimization, maximizing energy intake per unit time through reductions of travel times to foraging areas or/and increases in energy gain during foraging by targeting prey of higher energy density or higher energy content per prey item. In the case of marine predators, animals generally disperse over broader ranges during the non-breeding period as there is no need for frequent returns to the colony to provision offspring (Bost et al. 2009b; Dunn et al. 2011; Thiebot et al. 2011). Release from central-place foraging during the non-breeding season may reduce energetic demands and may mean other foraging solutions are optimal.

Diving predators: a particular case of central place foraging

In the case of **diving predators**, foraging takes place in 3 dimensions and therefore needs to be optimized at the ocean surface as well as at depth. Depending upon their physiology, diving predators can spend extended periods under water (Kooyman & Campbell 1972; see review in Kooyman 1989; Boyd 1997; Thompson & Fedak 2001; Green et al. 2005; Halsey et al. 2006). While the depletion of oxygen resources is the main factor limiting underwater time in air-breathing diving predators (see review in Boyd 1997), considerable variation in dive duration with most dives ending before the estimated aerobic dive limit (Jodice & Collopy 1999; Sparling et al. 2007) indicates that the quality of the prey resource encountered during the dive may significantly impact diving behaviour (Thompson & Fedak 2001; Mori & Boyd 2004; Sparling et al. 2007). In the context of foraging theory, diving predators can be seen as central foragers departing from the surface, where dive depth will represent the distance to the food patch and bottom duration will reflect the time

spent feeding within the patch (Houston & McNamara 1985; Houston & Carbone 1992). The observed foraging behaviour of a diving marine predator is therefore likely to be the result of behavioural adjustments in the 3 dimensions of the ocean, where energy intake per unit time should be optimized in both dimensions. Increasing constraints on the forager should lead to increases in foraging optimization of surface movements as well as diving behaviour.

Optimal foraging theory and the way tests of the theory have been carried out have been criticized (Pierce & Ollason 1987) and have to be considered when evaluating potential adaptations and evolution of animals in the light of foraging optimization. Optimal foraging strategies may not occur in nature, as animals may still track fitness maxima in a variable environment rather than having arrived at an optimum in a static environment. Another criticism of optimal foraging theory is that it is impossible to test the existence of optimal foraging strategies, as the reward an animal is seeking when showing a certain behaviour can not be identified by the researcher, and the function of a displayed activity can not be assumed to be known a priori.

1.2 Environmental heterogeneity and variability

The structure of the environment and the distribution of resources in space and time are not uniform, but show considerable variability across both time and space (Kotliar & Wiens 1990). Spatial and temporal variability of environmental conditions, including for basic resources such as nutrients, directly impact the distribution and abundance, and consequently the availability of prey resources for foragers exploring such a heterogeneous environment (Stenseth et al. 2002). Resource variability therefore affects marine predators via foraging performance translating into breeding performance and fitness, and consequently natural selection and population growth. Foraging ecology explicitly

integrates such habitat heterogeneity, by extending the isolated study of the forager's behaviour and the optimization of its energy gain by considering foragers moving through a variable environment of patchy resource distribution, where foragers have to adjust their behaviour in order to optimally explore prey resources characterized by such spatio-temporal variability (Fauchald & Tveraa 2003; Wilson et al. 2005). Spatial and temporal resource variability have different impacts on foraging strategy and performance, and are most easily considered in isolation before considering their combined effects on marine predators foraging.

1.2.1 Spatial habitat variability

The earth system is characterized by high levels of heterogeneity in physical, chemical and biological patterns (see review in Kleidon 2010). This heterogeneity ultimately results from geological variation and spatial and temporal differences in the absorption of solar radiation by the earth, leading to temperature gradients in the atmosphere and ocean (Kleidon 2010). Such temperature patterns themselves already play an important role in defining suitable conditions for biological and ecological processes, or suitable habitats for species (Peck et al. 2004; Pearson et al. 2006). However, these gradients also drive the atmospheric and oceanic circulation, providing the means to transport heat and geochemical elements within the earth system (Giorgi & Avissar 1997; Kleidon 2010), which leads to further increases in physical habitat heterogeneity and therewith heterogeneity in resources distribution and biological patterns. While such heterogeneity corresponds to a state far from the thermodynamic equilibrium of the earth system (Lovelock 1965), it is a crucial condition for maintaining environmental and ecological processes and cycles of the earth system (Schroedinger 1944). Habitat heterogeneity is one of the cornerstones of ecology (Simpson 1949; MacArthur & Wilson 1967; Tews et al. 2004), governing patterns of species diversity, behaviour and population development.

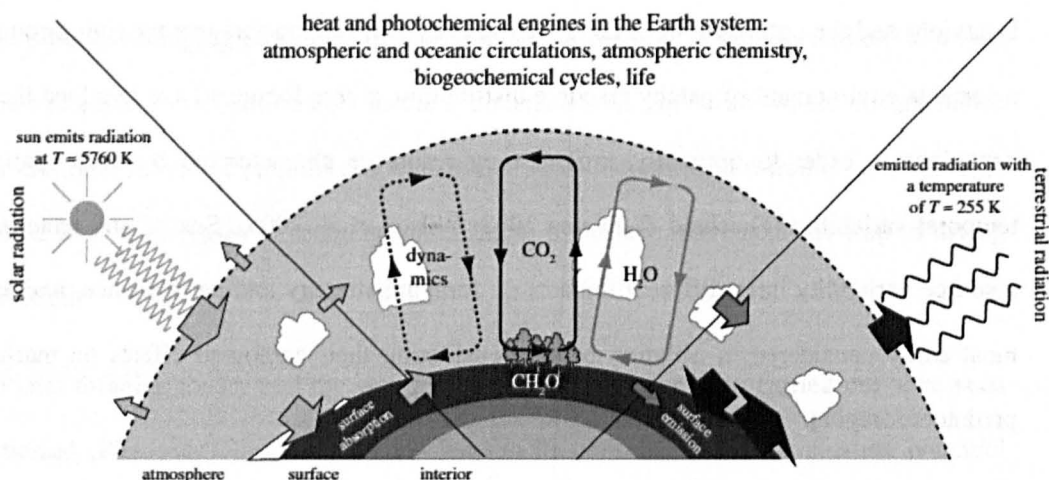


Figure 1.1: The thermodynamic context of environmental and ecological systems. The cycling of matter at the planetary scale – as manifested by a strong atmospheric circulation and the global cycles of water and carbon – require engines to continuously operate to keep these cycles running. These engines ultimately run on gradients of radiative fluxes, which result from the vastly different radiative temperatures of the Sun and Earth. Gradients in radiative fluxes can result in gradients of heating, which drive heat engines such as the atmospheric circulation. Figure from Kleidon (2010).

Foraging in a heterogeneous environment

In the context of foraging, habitat heterogeneity plays an important role, as prey distribution is directly dependent on the distribution of resources in the environment. Such spatial patterns of prey distribution are a key factor influencing predator movements and their foraging strategy (Pyke 1984; Fauchald et al. 2000; see review in Fauchald 2009). In general prey resources are considered to be distributed in patches of variable size and density, where a patch is defined as a spatially limited zone containing a finite quantity of resources in a generally poorer environment. These patches are distributed in space in a random or non-random way (Wiens 1989; Fauchald 1999) depending on the structure of the environment and dynamic processes governing such structure. In this spatially heterogeneous but structured environment predators have to develop strategies to optimally

explore the prey landscape of patches organized at different scales. In a zone of high prey abundance, a predator is expected to adapt its behaviour in terms of reducing travel speed and increasing the sinuosity of the movements. This assumption is based on the prediction of optimal foraging theory that a predator having already captured the first prey item in a new putative patch, should intensify its foraging effort in the patch encountered (Charnov 1976; Parker & Stewart 1976).

Such behavioural response increases residency time of the forager within the prey patch, ensuring that the animal is more likely to fully exploit a prey patch because its behaviour reduces the

chances of it leaving the patch, ultimately leading to higher prey capture rates. The resulting behaviour is called “Area-Restricted Search” (ARS, Kareiva & Odell 1978), which is defined by a decrease in speed and an increase in sinuosity of movements within a prey patch (Benhamou & Bovet 1989). Between two patches, the forager travels more linearly and at a faster speed. Based on these assumptions, track-based measurements of the movements of free-ranging predators are thought to provide information on their foraging behaviour. The scales of the ARS behaviour reflect the forager’s movement adjustments to the scales of spatial and temporal variability of the prey patches encountered.

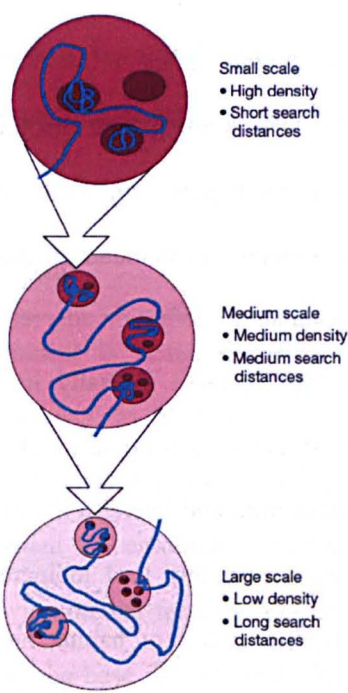


Figure 1.2: Hierarchical patch system with high-density small-scale patches (dark red) nested within low-density large-scale patches (light red). Blue line is the search pattern of a forager using a nested area-restricted search. Figure from Fauchald (2009).

Habitat heterogeneity is an important factor for foraging, assuming that structurally complex habitats might provide more niches, and therefore more diverse ways of exploiting the environmental resources to foragers. A niche in the context of foraging means here the hypervolume in the multi-dimensional space of ecological variables within which a species can maintain profitable foraging, which is necessary for maintaining a viable population (definition adapted from Hutchinson 1957). More niches available to the forager may increase diversity in foraging behaviour and possibilities of optimizing foraging strategies depending on physiological and seasonal constraints on the animals. It may reduce intra- and interspecific competition (Pianka 1981; Svanback & Bolnick 2005), which may ultimately lead to increased foraging performance and population growth. However, the effects of habitat heterogeneity may vary considerably depending upon whether structural attributes are perceived as heterogeneity or fragmentation (Tews et al. 2004), which may have contrasting effects on foraging. Such perception may vary from species to species depending upon their foraging requirements, but also within a species depending upon the constraints of the animals, impacting their time and energy budget. For example, prey patches with high-level fragmentation but containing highly profitable resources (in terms of accessibility, density and/or energy content of the prey items) may represent favourable conditions for foragers under low constraint with sufficient time to travel between the patches, where foraging within a patch may be highly profitable. For foragers under higher constraints with less time available for travelling and search for new prey patches, less fragmented prey may represent better foraging conditions, even if prey resources within such a larger patch may be less profitable in terms of accessibility, density or energy content per prey item. Foraging decisions in a given environment are therefore likely to be a compromise between spatial constraints such as the distance of the resources to the colony, and its suitability to the animals' constraints in terms of resources profitability and fragmentation. A diverse environment characterized by elevated

heterogeneity and distinct environmental niches is likely to provide for a higher range of choices for the animal, allowing for better adjustment in foraging behaviour and a more optimized foraging strategy according to the prevailing constraints and prey distribution at different spatial scales.

The marine environment and its patchy resource distribution

Despite its apparent uniformity, the marine environment is characterized by strong heterogeneity in terms of both physical parameters as well as biological productivity (Bainbridge 1957; Martin et al. 2002). Spatial patterns in physical properties of the water masses, such as temperature and salinity, as well as nutrient concentration in the horizontal and vertical dimension, are largely determined by environmental features such as ocean currents and their interaction with bathymetry, forming the base for heterogeneity in the ocean. Nutrients and light are the limiting factors in primary productivity, and determine patterns of phytoplankton growth in the ocean (Marra 1978). Areas of enhanced mixing and nutrient input into the upper water column, such as bathymetry-related upwelling as well as fronts and eddies, represent zones of enhanced biological productivity (Eppley & Peterson 1979; Longhurst & Glen Harrison 1989). Furthermore physical processes such as horizontal and/or vertical convergences (Hunt 1990), or the barrier effect of vertical physical gradients (Boyd & Arnbom 1991) may lead to the passive aggregation of biomass at such features. Phytoplankton is at the bottom of the marine foodweb, directly impacting the distribution and abundance of higher trophic levels (“bottom-up control”, Frederiksen et al. 2006). The distribution of marine resources, including the prey for marine predators, is therefore determined by the physical environment as well as oceanographic processes and their interaction with bathymetry.

Foraging strategies of marine predators in a patchy environment

Such heterogeneity in the oceanographic environment, and therefore prey resources, occur in the horizontal and vertical dimension of the ocean. Consequently, marine predators have to adjust their foraging behaviour at the surface and at depth in order to optimally explore prey patches. At the surface, structuring in the marine environment occurs at different scales, ranging from filaments at sub-mesoscale (scales of metres), to fronts and eddies at the mesoscale (1-300 km), up to large basin-wide scales (hundreds to thousands of km) (Mann & Lazier 1996; Martin et al. 2002). These environmental structures at different

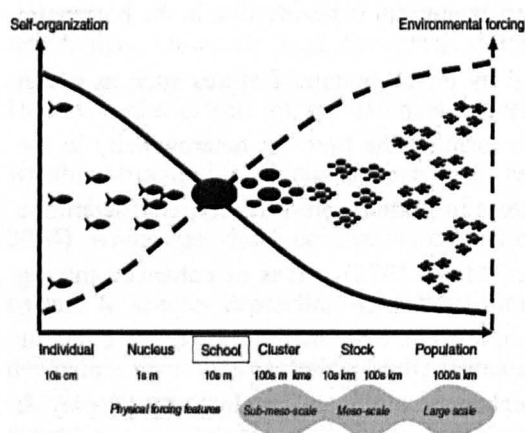


Figure 1.3: A conceptual model describing the relative importance of factors regulating aggregations of gregarious fish as a function of scale. There are two x-axes, one based on self-organisation, and the other on environmental forcing. The importance of these on fish distribution depends on the spatial scale. At smaller scales, self-organisation mechanisms are likely to be dominant; at larger scales adaptations and response to the environment are more important. Figure from Bertrand et al. (2008).

scales are thought to be key factors determining aggregative patterns of fish (Bertrand et al. 2008), which in turn are important prey resources for foraging marine predators. In the context of marine predators foraging, mesoscale features such as fronts and eddies have been reported to play key roles, as they appear to provide for profitable foraging zones for various marine predators (see review in Bost et al. 2009a). Frontal zones are often characterized by elevated biomass compared to interfrontal zones (Lutjeharms et al. 1985; Pakhomov et al. 1994) due to increased primary productivity as well as biomass concentration by convergence processes (Schneider 1990; Hunt 1990; Spear et al. 2001). Such biomass accumulation may attract higher trophic levels including prey for marine predators. In the vertical dimension, water masses of distinct physical properties as well as

physical gradients between such water masses are important elements for heterogeneity and structuring. Different water masses may provide for suitable habitats for different prey species, and discontinuities in physical properties in the water column may result in enhanced biological activity due to the barrier effect of the density gradients leading to a concentration of sinking matter (Boyd & Arnbom 1991). These nutrient-rich water layers may result in increased primary productivity and attract higher trophic levels including prey for marine predators. In particular, the thermocline is known to be of considerable importance for marine predators (Boyd & Arnbom 1991; Cayre & Marsac 1993; Kitagawa et al. 2000; Charrassin & Bost 2001; Spear et al. 2001; Biuw 2007; Weng et al. 2009; Scheffer et al. 2012) as it provides for potential biomass accumulation for various trophic levels at relatively shallow depths. However, physical gradients at greater depths may also play important roles in structuring the water column and providing locations for prey aggregation for marine predators depending upon their physiological dive capacities, as suggested by Muelbert et al. 2012 for elephant seals.

Marine predators have to adjust their foraging behaviour in response to heterogeneity in oceanographic structures and associated prey aggregations at different scales in the horizontal and vertical dimension in the ocean. The foraging performance of a marine predator may therefore be a compromise of behavioural adjustments of surface as well as diving behaviour in order to optimize its exploration of a 3-dimensional prey field. In this context, habitat heterogeneity with high levels of segregation and the presence of distinct foraging niches may play a key role for optimizing foraging strategy in the horizontal and vertical dimension of the ocean. Under natural selection, marine predators have evolved strategies to optimally explore heterogeneity in habitat and prey distribution in the ocean, and breeding colonies may have evolved in close proximity to the best foraging conditions for a given species in terms of spatial availability of prey resources. In this context,

pressure from predation may also play an important role, and animals' breeding colonies may finally emerge and evolve as a compromise of both these key factors.

1.2.2 Temporal habitat variability

The structures defining spatial heterogeneity of resources in the environment are subject to temporal variability at different temporal and spatial scales and of different magnitude. The atmospheric circulation is characterized by well-defined patterns (e.g. Walker cells, wind systems), which are subject to variability at different spatial (regional and global) and temporal (daily, seasonal, multi-annual, decadal) scales. Multiple climate indices exist to characterize atmospheric variability and integrate several environmental variables. The most important ones are the El Niño– Southern Oscillation (ENSO), the North Atlantic Oscillation (NAO) and, in the Southern Hemisphere, the Southern Annular Mode (SAM) (see review in Stenseth et al. 2003), but there are regional climate indices that describe climate patterns on smaller spatial and temporal scales (Indian Ocean Dipole, South Atlantic Dipole).

Such atmospheric variability impacts oceanographic patterns in the ocean (Terray & Dominiak 2005; Sallée et al. 2008; Sallée et al. 2010), and therefore also prey distribution for marine predators. However, optimal foraging theory requires a certain stability and predictability of resources in the foraging areas explored. The adjustment of foraging strategy and habitat selection by marine predators partly depends upon their knowledge about the environment and their previous experience (Weimerskirch 2007; Hamer et al. 2007). For successful foraging, they therefore rely upon oceanographic structures of a certain recurrence in time and space, leading to predictability of the structure and associated prey resources.

Predictability of profitable structures in the marine environment

The predictability of environmental structures and associated prey resources is thought to be related to the spatial scale of environmental structure as well as to the scale of temporal variability impacting the structure. For example, fronts and eddies are large- and mesoscale features of the marine environment, which are thought to host important prey resources for marine predators. Spatial stability and temporal recurrence of these structures make them predictable locations of potentially high prey densities at large and mesoscales (Hunt et al. 1999). Between oceanographic features occurring at large spatial and temporal scales and small-scale structures of high spatial and temporal instability and apparently random prey distribution, structures of spatially and temporally predictable prey aggregations at mesoscales such as fronts and eddies are thought to be of particular importance to foraging marine predators (Pinaud & Weimerskirch 2005).

Climate change: a new challenge for marine predators

Such temporal variability, including the occurrence of extreme events, is inherent in the earth's system, and marine predators and other organisms and structures have evolved in this fluctuating environment and are able to adjust their foraging behaviour at the corresponding scales (Pinaud & Weimerskirch 2005; Weimerskirch 2007). However, global warming (Gille 2002) and the associated increase in environmental stochasticity (Alley et al. 2003) may represent new challenges for marine predators' foraging and population survival (see review by Grémillet & Boulinier 2009).

Warming in ocean temperatures (Gille 2002; Solomon et al. 2009) may lead to shifts in prey species habitats, and lead to mismatch of such resources and the locations of marine predators' breeding colonies. Furthermore changes in atmospheric patterns may impact oceanographic conditions, and therefore the distribution of marine resources. Climate modes such as ENSO and SAM have been reported to change in terms of patterns and magnitude (Fogt & Bromwich 2006), which may impact environmental patterns on a

global scale. The increase in temperature is also thought to increase environmental stochasticity (Alley et al. 2003), and therefore the occurrence of extreme events (Jentsch et al. 2007; Solomon et al. 2007; Jentsch & Beierkuhnlein 2008). These changes may represent new challenges for marine predators' foraging and population survival (Trathan et al. 2007). Changes in key oceanographic structures of foraging such as deepening of the thermocline (Sallée et al. 2010), or increased match-mismatch of prey resources and predator distribution may make it increasingly difficult for marine predators to keep foraging in an optimal way, and to acquire sufficient resources over critical time scales. Marine predators are known to show flexibility in foraging behaviour and capacities of adaptation to variability in environmental conditions and prey distribution by spending more time foraging in poor years (Piatt & Sydeman 2007; Harding et al. 2007; Ronconi & Burger 2008) or adjusting the foraging areas explored (Péron et al. 2012). However, thresholds of such foraging flexibility may exist, where foraging profitability and reproductive success can no longer be buffered against low food availability in the foraging area (Dall & Boyd 2002). Climate change may therefore have drastic impacts on the foraging success, distribution and population development of marine predators (Croxall et al. 2002; Forcada et al. 2005; Murphy et al. 2007a; Trathan et al. 2006, Trathan et al. 2007; Forcada & Trathan 2009; Ballard et al. 2010; Hazen et al. 2012).

In the case of marine predators in the Southern Ocean, the change of large-and mesoscale patterns such as ACC frontal zones positions and dynamics as well as mesoscale structures such as eddies (Thompson & Solomon 2002; Sallée et al. 2008; Sallée et al. 2010) may affect the horizontal and vertical distribution and abundance of prey in proximity of breeding colonies. This is likely to impact the foraging success and fitness of marine predators, which is ultimately translated into population development. Investigation of key structures where predators forage successfully is therefore an important issue to investigate in order to better understand marine predator behaviour, and to evaluate potential impacts

of a changing environment on their behaviour and population development. The occurrence of extreme events in terms of environmental conditions, marine predators' behaviour and breeding success may allow insights into reactions of these animals to extreme conditions, and may indicate potential reactions and adaptations to future environmental change.

1.3 The Southern Ocean

The Southern Ocean is distinguished from all other oceans in that it encircles the globe without being diverted by continental barriers. Its main hydrographic feature is the Antarctic Circumpolar Current (ACC, Rintoul et al. 2001), a powerful eastward flowing, wind driven current circling the Antarctic continent, forming a circumpolar connection between 3 ocean basins. The Southern Ocean comprises the southern parts of the Pacific, Atlantic and Indian Ocean and represents approximately 20% of the World's Ocean (Deacon 1937). Its northern limit is defined by the Subtropical Front (STF), an oceanographic feature that is characterized by rapid changes in SST and salinity over short spatial scales, marking the transition between warm and salty subtropical waters and cooler, fresher waters to the south (Deacon 1937; Deacon 1982); the STF is generally situated between 35°S and 45°S (Orsi et al. 1995).

The ACC is mainly driven by the prevailing strong westerly winds and the Coriolis force (Trenberth et al. 1990); it represents one of the largest currents in the world, carrying roughly $135 - 147 \times 10^6 \text{ m}^3 \text{ s}^{-1}$ of water around Antarctica (Cunningham et al. 2003; Rintoul & Sokolov 2001). As such, the ACC is a critical component of the global climate system, allowing the transfer of heat and water between the ocean basins and therefore around the globe.

The path of the ACC flow is strongly influenced by the steering effect of bottom topography (Sverdrup 1942; Marshall 1995). This bathymetric steering effect is particularly important at the high latitudes of the Southern Ocean where the ocean is weakly stratified, and currents near the ocean surface align in roughly the same direction as deep ocean currents, consequently often following pronounced depth contours (Schulman 1975; Gille et al. 2000). Such bathymetric steering of ocean currents occurs particularly in

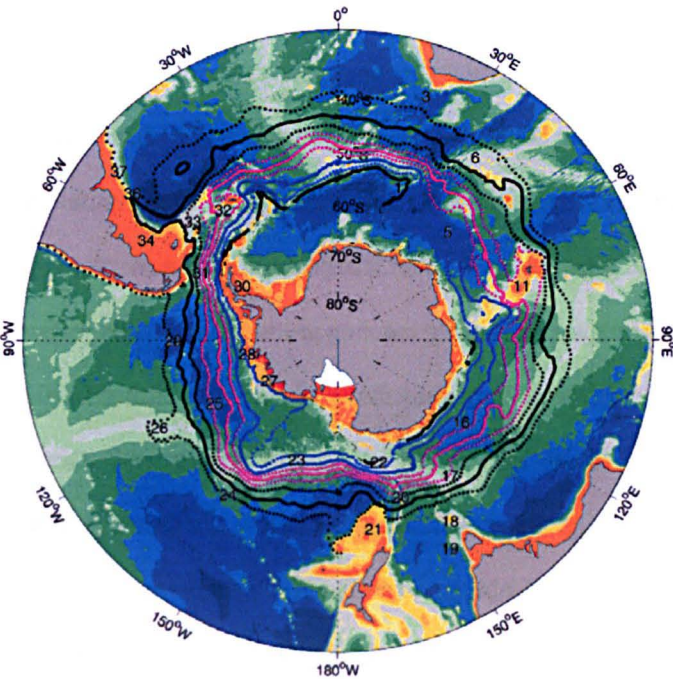


Figure 1.4: The Southern Ocean with the Antarctic Circumpolar Current (ACC). The ACC fronts are colour coded from north to south as follows: black-SubAntarctic Front (SAF); magenta – Polar Front (PF); blue – southern ACC Front (SACCF); black – Southern ACC Boundary (SB). Frontal positions are determined from Sea Surface Height (SSH). The ACC fronts overlie the SO bathymetry. Figure from Sokolov & Rintoul (2009a). For the numbers of the bathymetric features see Sokolov & Rintoul (2009a), Figure 6.

proximity to the major topographic features within the ACC flow, such as the Scotia Arc and the extensive Kerguelen Plateau (Marshall 1995). In the context of this study the northward deviations of the southern parts of the ACC caused by the South Sandwich Islands Arc at ~30°W and at the Kerguelen Plateau at ~70°E are of particular importance for the oceanography in close proximity to our study areas at South Georgia and Kerguelen (Orsi et al. 1995; Thorpe et al. 2002a; Thorpe et al. 2004).

The ACC includes four major circumpolar fronts south of the STF, which are, from north to south, the SubAntarctic Front (SAF), the Antarctic Polar Front (PF), the southern ACC Front (SACCF) and the Southern Boundary of the ACC (SB) (Orsi et al. 1995; Belkin & Gordon 1996). Fronts are zones that separate distinct surface water masses and are characterized by strong horizontal gradients in physical water properties such as temperature, salinity and density (Schneider 1990). In the vertical dimension, frontal zones are furthermore characterized by changes in the structure of the water column due to the presence of different water masses (Orsi et al. 1995, Belkin & Gordon 1996; Trathan et al. 1997; Trathan et al. 2000; Park et al. 1998; Thorpe et al. 2004; Boehme et al. 2008a; Venables et al. 2012). Frontal positions can thus be identified based on ocean surface parameters such as SST (Park et al. 1993; Orsi et al. 1995; Belkin & Gordon 1996), SST gradient (Moore et al. 1999b) or SSH and geostrophic velocities (Sokolov & Rintoul 2009; Venables et al. 2012) as well as by their subsurface expressions in the water column (Park et al. 1998; Boehme et al. 2008a; Sokolov & Rintoul 2009; Venables et al. 2012). For example the PF can be defined by the 5°C isotherm at the surface during summer (Park et al. 1993) or, more accurately, by the northernmost extent of WW at 200m depth (Park et al. 1998). While frontal positions based on different criteria are mostly in agreement, the frontal properties are not uniform in all sectors of the Southern Ocean, and the variation in frontal structure from region to region and the multiplicity of definitions used by various authors have led to some confusion in the determination of ACC frontal positions.

The zones between the ACC fronts are characterized by lower dynamics, leading to reduced mixing and therefore increased stability in hydrological structures. From north to south, the ACC interfrontal zones are referred to as the Subantarctic Zone (SAZ, between the STF and the SAF), the Polar Frontal Zone (PFZ, between the SAF and the PF), the Antarctic Zone (AAZ, between the PF and the SACCF), and the Southern Zone (SZ, between the SACCF and the SB) (Orsi et al. 1995).

In the vertical dimension, the Southern Ocean is well structured by different water masses characterized by distinct physical properties, and by the physical gradients between these water masses. During the austral summer, the water column between the PF and the SACCF is characterized by the Surface Mixed Layer (SML) and the underlying cold Winter Water (WW) originating from the previous winter mixed layer capped by seasonal warming and freshening within the SML (Park et al. 1998). WW properties are continuously altered by vertical mixing processes with the surrounding warmer water masses, which may vary according to oceanographic processes such as upwellings or eddies. WW properties may therefore show important spatial variability (Park et al. 1998). The SML and WW are separated by a thermocline, a strong vertical temperature gradient of variable extent and intensity depending on the SML and WW properties as well as on physical mixing processes. Below the WW layer is the Circumpolar Deep Water (CDW), which is characterized by an oxygen minimum and a temperature maximum. CDW is the most voluminous water mass in the Southern Ocean (Worthington 1981) carried eastward by the ACC. Situated below the WW and therefore not directly in contact with the atmosphere, it does not experience the winter cooling and summer warming of the WW and SML, and may be less directly impacted by atmospheric variability (Jacobs & Georgi 1977). The mixing of CDW with the WW has been suggested to provide for important nutrient input into the upper water column, particularly in locations where interactions with bathymetry occur, for example where CDW meets the Antarctic shelf such as in the Ross Sea and in the WAP (Dinniman et al. 2011). The mixed layer where CDW mixes with WW has been identified as a distinct water mass, often referred to as modified CDW, or mCDW (Gordon et al. 2000).

1.4 Studying marine predator foraging behaviour

The study of wild animals in their natural environment is often challenging, as they live in habitats where direct observation is difficult or impossible. Biologging is the use of miniaturized animal-attached tags for recording data about the movements, behaviour, physiology and/or environment of free-ranging, undisturbed animals (Ropert-Coudert & Wilson 2005; Hooker et al. 2007; Ropert-Coudert et al. 2009a). In the marine environment, biologging allows the study of animals and their interaction with oceanography, which would not be accessible during their extended (sometimes exclusive) times at sea. In the case of diving predators, a small device is usually attached to the animals, recording, for example, surface locations (GPS and Argos devices) or behavioural and physical parameters during the dives (such as pressure for dive depth, ambient temperature, light, salinity for diving animals) (Time-Depth-Recorders, TDR). The deep dive depths of some species and the long at-sea times represent important constraints for the logging devices in terms of pressure resistance and memory while keeping the device as small as possible to minimize the impact on the animal.



Figure 1.5: King penguin with a tracking device attached.

1.4.1 Methods for the detection of foraging behaviour in marine predators

In the context of studying the foraging behaviour of marine predators, one of the challenges is to infer foraging activity from behavioural indices obtained by biologging methods. Diving predators move in a multi-dimensional framework (x, y, z and time, plus multiple environmental dimensions), whereas foraging may only be visualized in the horizontal and vertical. Fortunately, there exist various methods to identify the occurrence of foraging behaviour from biologging data at the ocean surface and at depth. From surface behaviour, foraging is sometimes detected based on the assumption that the animals change their movement behaviour between travelling and foraging, with changes from relatively linear movements at high speed during travel to ARS behaviour characterized by increased sinuosity and lower speed when exploring a prey patch (Bovet & Benhamou 1991; Benhamou 2004). Methods for the detection of foraging behaviour at the surface are based on various analysis methods such as First-Passage Time (Fauchald & Tveraa 2003), changes in the fractal dimension of the trajectory (Fritz et al. 2003; Tremblay et al. 2007) and residence time in a certain zone (Barraquand & Benhamou 2008). Furthermore there are process-based models, which allow predictions of the animals' behaviour along its trajectory based on previous behavioural states (State-space models, Jonsen et al. 2003; Jonsen et al. 2005; see review in Patterson et al. 2008 and Jonsen et al. 2012). However, such methods for detecting foraging behaviour from changes in surface movements need to be used with caution, with careful considerations of the spatial scale at which the foraging behaviour will be detected (Robinson et al. 2007). In addition to changes in surface behaviour, marine predators are likely to change their diving behaviour in response to prey availability (Houston & Carbone 1992; Thompson & Fedak 2001). Based on this assumption foraging can be detected from changes in diving behaviour, such as increasing dive rate within a prey patch (Dragon et al. 2010), the time spent in the bottom phase of a dive (Boyd & Arnborn 1991; Charrassin et al. 1999; Austin et al. 2006) as well as the

bottom time relative to the total dive duration (Halsey et al. 2007) or changes in residuals of absolute or relative bottom times (Bailleul et al. 2008). Furthermore the fine-scale behaviour at the bottom of a dive, where foraging is thought to take place, can give an indication of the feeding behaviour of the animal. These undulations or wiggles are small vertical movements of the animal during the bottom phase of the dive, which are thought to arise from prey capture and are therefore suggested to represent a reliable indicator for feeding (Simeone & Wilson 2003; Takahashi et al. 2004; Bost et al. 2007; Bost et al. 2008). The choice of an appropriate method for the investigation of marine predator foraging behaviour from the wide range of available possibilities, depends upon the question to be answered as well as on the temporal and spatial resolution of the available data.

1.4.2 Studying marine predator behaviour in the 3-dimensional oceanographic environment

Initial studies concentrating on the tracking of marine predator surface behaviour and its evaluation in combination with remotely sensed oceanography have allowed first important insights into the behaviour of marine predators at sea, and the importance of oceanographic features for foraging (Rodhouse et al. 1996; Bost et al. 1997; Guinet et al. 1997). However, recent advances in biologging with combined behavioural and in-situ oceanographic

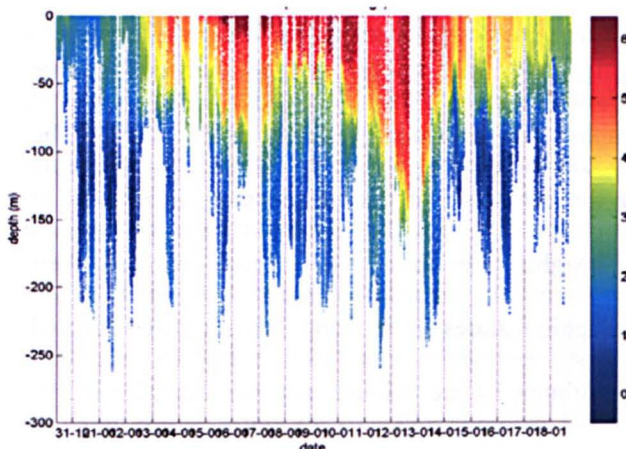


Figure 1.6: In-situ depth-temperature profile along the trajectory of a foraging king penguin obtained from a Time-Depth-Temperature Recorder (Mk9). The high temporal and spatial resolution of the data allows detailed insights into hydrological structures encountered by the penguin at depth. Cold water masses are shown in blue, warm in red.

measurements at high sampling rates (Ropert-Coudert & Wilson 2005; Hooker et al. 2007) have significantly increased the possibilities of studying the animals' behaviour in their environment, and to examine possible links between the animals' behaviour and oceanographic features at the ocean surface and in the water column (Charrassin & Bost 2001; Biuw et al. 2007; Biuw et al. 2010; Hooker et al. 2007; Costa et al. 2010; McIntyre et al. 2010; McIntyre et al. 2011; Bestley et al. 2012). The animal-borne tags collect oceanographic data at the scale and resolution that match the animals' behaviour, allowing for the study of the animals' behaviour in its immediate environment in high spatial and temporal detail.

The use of such tags furthermore allows the in-situ sampling of the oceanographic environment at detailed spatial and temporal scales. Marine predators can thus be used to collect oceanographic data on scales not possible with conventional methods (Lydersen et al. 2002; Hooker & Boyd 2003; Charrassin et al. 2004; Charrassin et al. 2008; Boehme et al. 2008a, Boehme et al. 2008b; Costa et al. 2008; Roquet et al. 2009). This is particularly interesting in areas such as the Southern Ocean, where the use of traditional ship-based surveys, remote-sensing systems and Argo-floats is limited. The use of oceanographic data from animal-borne sensors has significantly improved our understanding of key features in the Southern Ocean such as the ACC and associated oceanographic processes and features at the surface and at depth (Boehme et al. 2008a; Charrassin et al. 2008; Costa et al. 2008).

Such technical advances in biologging have lead to the synergy between marine behavioural ecology and oceanography (Ropert-Coudert & Wilson 2005). The interdisciplinary approach to studying the behaviour of marine predators in relation to oceanography has given important insights into how the animals explore their environment, and potential key oceanographic features for foraging. It has allowed detailed studies of the exploration of the water column by the animals, and the identification of

oceanographic features or specific water masses at depth targeted during foraging (Campagna et al. 2000; Charrassin & Bost 2001; Charrassin et al. 2004; Bailleul et al. 2007; Biuw et al. 2007; Muelbert et al. 2012). For example, the use of temperature and salinity data collected by seals foraging at the Western Antarctic Peninsula has provided detailed insights into the 3-dimensional habitat use of different seal species (Burns et al. 2004; Costa et al. 2010). The data have given new detailed information about circulation patterns of CDW onto the Antarctic shelf, and its exploration by the seals (Costa et al. 2008; Costa et al. 2010), revealing inter-specific habitat segregation in terms of foraging areas explored as well as water masses targeted at depth (Costa et al. 2010). Furthermore the comparison of elephant seals at different breeding locations have allowed insights into fine-scale differences in habitat use, providing possible explanations for differences in foraging performances (Biuw et al. 2010).

Results from biologging studies suggest that the foraging of marine predators is strongly associated with oceanographic features such as fronts, eddies, specific water masses and thermal gradients in the water column, or bathymetry-related upwellings at shelf breaks or seamounts, where prey availability may be increased (Hunt 1990; Rodhouse et al. 1996; Bost et al. 1997; Tynan 1998; Lea & Dubroca 2003; Cotté et al. 2007; Trathan et al. 2008; Scheffer et al. 2010; Péron et al. 2012; Muelbert et al. 2012). These oceanographic features are thought to represent locations of high prey predictability and availability and therefore important foraging areas for marine predators. Spatial patterns and temporal variability of these features are impacted by environmental variability and are thought to be affected by climate change. Investigating the potential impact of climate change on marine predators therefore requires the identification of the oceanographic features on which animals rely, detailed knowledge about how animals explore these features in the horizontal and vertical dimension, as well as information about how these features may change. In this context, the comparative study of a marine predator in different breeding locations may allow

insights into how the animals adjust their foraging behaviour to different environments, and how the exploration of potential key oceanographic feature may impact foraging behaviour and performance.

Marine predators sit at or near the top of the marine food web, and as they consume large amounts of biomass from lower trophic levels, they integrate spatial and temporal patterns in the distribution and abundance of lower trophic levels; they have been proposed as representing important bioindicators of marine resources (Furness & Greenwood 1993; Boyd & Murray 2001; Bost et al. 2008). Such indications on spatial and temporal patterns of resources may be important to monitor and better understand

the variability of biological resources, particularly those at mid-trophic levels such as krill and myctophids which are difficult to assess, given the spatial and temporal variability of the environment. In this context, changes in marine predators' foraging behaviour may give important indications about spatio-temporal changes in marine foodweb.



Figure 1.7: A generalized Southern Ocean foodweb from the level of krill up to marine top predators. Four main size groups of animals are shown, each in a coloured ellipse. Figure from Rintoul et al. (2012).

1.5 PhD objectives and thesis structure

The overall objective of this PhD is to describe the foraging behaviour of a top diving predator of the Southern Ocean, the king penguin, breeding at both South Georgia and Kerguelen in relation to regional oceanographic features and variability in their horizontal and vertical dimension. In using a multi-site study, I envisage that I will be able to infer generic behavioural foraging attributes for my study species. I have approached this question by combining behavioural information regarding the penguins' surface and underwater movements with oceanographic data (remote sensing and in-situ measurements from biologging devices attached to the animals) in the horizontal and vertical dimensions at different spatial and temporal scales. This thesis is therefore situated at the interface of behavioural biology, ecology and oceanography, and attempts to integrate these disciplines in order to allow comprehensive insights into how these animals explore their environment.

The work for this PhD thesis has been **structured** and approached in the following way:

As a first step, I describe the foraging behaviour of king penguins in relation to oceanographic features at both breeding locations (Chapters 3 and 4). Building on previous work on king penguins foraging behaviour from both study sites I attempt to gain a more complete picture about how the penguins explore the oceanographic habitat in the horizontal and vertical dimension depending on the oceanography of the study sites. For this I first studied the spatial at-sea distribution of foraging king penguins in relation to oceanographic features in their foraging areas. I then investigated their behaviour in the water column and tried to find out key structures or water masses explored during foraging. This gave a 3-dimensional image of how king penguins explore the ocean, and what may be important oceanographic features explored during foraging in the foraging ambit of the breeding colony.

In **Chapter 3** I describe the foraging behaviour of king penguins breeding at South Georgia in relation to oceanographic patterns in their foraging area at the ocean surface and at depth. Previous studies of the foraging behaviour of king penguins at South Georgia (Trathan et al. 2008; Scheffer et al. 2010) have concentrated on birds during the incubation stage and did not consider brooding birds or detailed aspects of diving behaviour in relation to vertical oceanographic features. To gain a more complete picture about king penguins' foraging at South Georgia building on these previous results, I studied the foraging behaviour of the penguins during the brooding stage in relation to horizontal oceanographic features, and further focussed on the fine-scale exploration of the thermal structure of the water column by the penguins in the different frontal zones explored depending on their breeding constraints.

In **Chapters 4, 5 and 6** I describe the foraging behaviour of king penguins breeding at Kerguelen. Given a more extensive Kerguelen dataset it was possible to take into account spatial as well as temporal variability in oceanographic conditions and the penguins' behaviour. Furthermore the catastrophic breeding season of 2009/10 with an unprecedented impact on the Kerguelen king penguin behaviour and reproductive success required separate analyses and considerations. My work on king penguins breeding at Kerguelen is therefore subdivided in 3 chapters. In **Chapter 4** I explore the general foraging patterns of breeding king penguins from Kerguelen in relation to oceanographic patterns in their foraging area (building on previous studies on foraging king penguins at Kerguelen mainly during the brooding stage, see Charrassin et al. 2002; Charrassin et al. 2004; Bost et al. 2004; Bost et al. 2011). In **Chapter 5** I examine the particular situation during the breeding season 2009/10 when 94% of monitored birds failed to raise chicks. Finally, in **Chapter 6** I explore the general impact of environmental variability on the foraging behaviour of king penguins breeding at Kerguelen.

My study of king penguins in relation to their oceanographic environment across two study locations, allowed me to gain detailed insights into how these animals explore the ocean, and what oceanographic features may be of key importance for their foraging in both locations. While it is important to study an animals' behaviour in relation to the particular conditions close to the breeding site, it is important to remember that it remains difficult to evaluate to what extent the observed behaviour might be an adaptation to the particular conditions at that breeding site in that year, as opposed to how much the animals may have adapted to different environmental conditions at the two sites. Several studies have shown that the presence of a species in a given habitat may be closely linked to keystone structures, where such a keystone structure is defined as a distinct spatial structure providing resources, shelter or "goods and services" for a species (Tews et al. 2004). Detecting crucial keystone structures of a species may be of key importance for a better understanding of the animals' foraging strategies and behavioural patterns emerging under different environmental conditions.

In **Chapter 7** I consider a number of broader issues developed from the discussion of Chapter 3 – 6. This involves as a comparison of the two study locations, where I try to combine the results of the separate study locations into a set of conclusions about more general foraging patterns of king penguins in relation to their oceanographic environment. In this context, I considered the importance of the location of the breeding colony in relation to the Polar Front, which determines how the foraging animals may cope with the local conditions associated with this key oceanographic feature and the vertical thermal structures associated with other Antarctic Circumpolar Current (ACC) fronts and zones. Based on the results of this comparative approach I end by finally discussing potential reactions of king penguins to future environmental change and how potential key oceanographic features used by king penguins foraging may change, and how the penguins may be able to adjust their foraging behaviour to such changes.

Chapter 2

Study location, study species and methods



2.1 The study locations: Oceanography around South Georgia and Kerguelen

The islands of South Georgia and Kerguelen are situated within the flow of the Antarctic Circumpolar Current (ACC), respectively in the Atlantic and Indian Ocean sectors of the Southern Ocean. South Georgia is located to the south of the Polar Front (PF), whereas Kerguelen is situated just to the north of the PF (Orsi et al. 1995; Park et al. 1998; Moore et al. 1999b; Sokolov & Rintoul 2009; Park & Vivier 2011). Both islands are situated in close proximity to the highest bathymetry in the flow of the ACC, steering the ACC after it exits the Drake Passage and flows over the Scotia Arc in the Atlantic and over the Kerguelen Plateau in the Indian Ocean (Marshall 1995; Moore et al. 1999; Park et al. 2008b; Sallée et al. 2008).

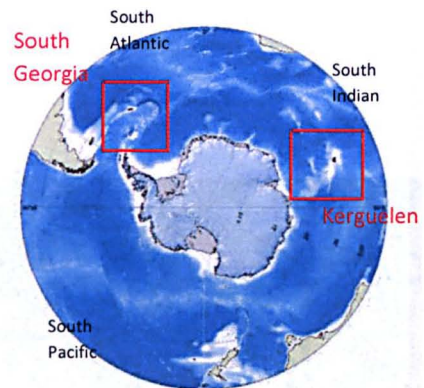


Figure 2.1: Locations of the study sites South Georgia and Kerguelen in the Southern Ocean. White shading shows major bathymetric features.

Areas downstream of locations where there are strong interactions of the ACC with bathymetry, are characterized by persistent patterns of increased biological productivity from bathymetry-related nutrient upwelling and downstream advection (Sokolov & Rintoul 2007), which may maintain highly productive ecosystems and rich foodwebs in these locations. Islands situated in such conditions therefore provide favourable breeding locations with profitable foraging grounds for land-based marine predators. The Scotia Sea and the Kerguelen Plateau are two of the most productive areas in the Southern Ocean (Charrassin et al. 2004; Holm-Hansen et al. 2004; Blain et al. 2007; Murphy et al. 2007b; Tarling et al. 2012; Park et al. 2010; Dragon 2011; Whitehouse et al. 2012), with the interaction of the ACC with bathymetry being a major factor for allowing high levels of

biological productivity (Park et al. 1998; Park et al. 2008b; Blain et al. 2007; Murphy et al. 2007; Mongin et al. 2008) and supporting extensive colonies of marine land-based predators such as seals, penguins and other seabirds (Boyd et al. 2002; Murphy et al. 2007; Hindell et al. 2011; Park & Vivier 2011).

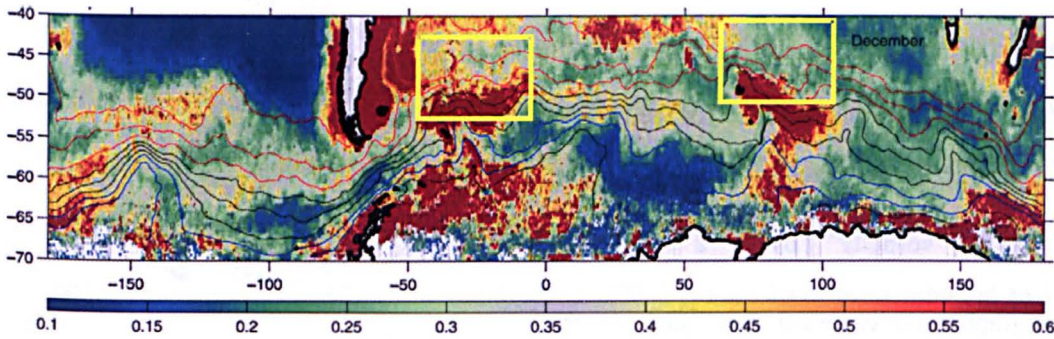


Figure 2.2: Primary productivity (remotely sensed Chlorophyll-a concentration) during December in the Southern Ocean. Yellow boxes indicate the locations of the Scotia Sea and the Kerguelen Plateau. Figure from Sokolov & Rintoul (2007).

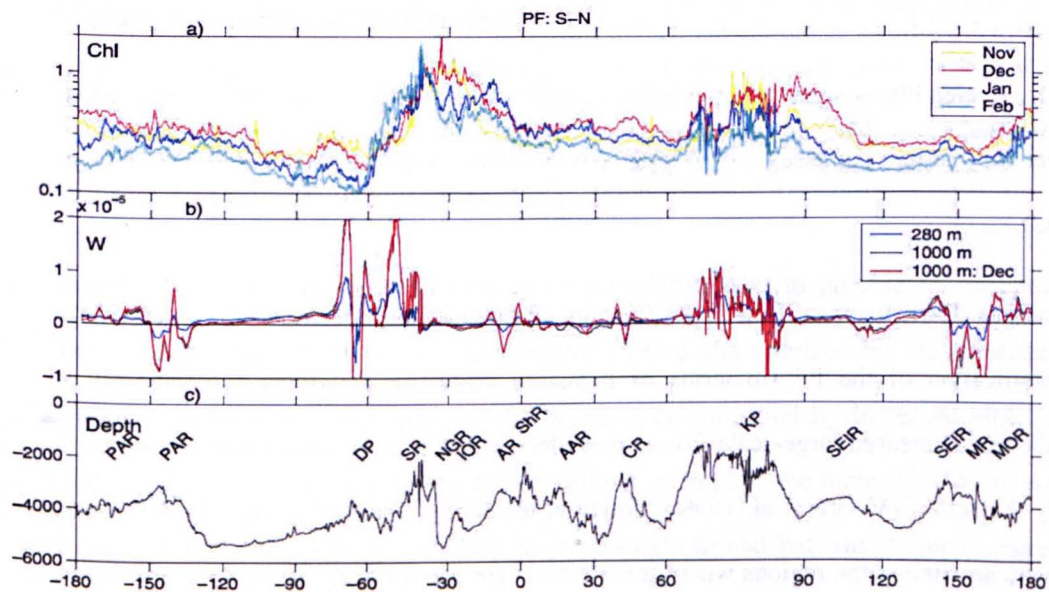


Figure 2.3: Primary productivity (a), vertical velocity (b) and ocean depth (c) in the Southern Ocean, averaged between the northern and southern branches of the Polar Front. Highest primary productivity occurs in the Scotia Sea and over the Kerguelen Plateau, coinciding with regions of rugged bathymetry and high vertical velocities in the ocean. Figure from Sokolov & Rintoul (2007).

In both locations, parts of the eastward flow of the southern ACC shows significant deviations to the north and therewith into areas close to the islands (Marshall 1995; Orsi et al. 1995). Such large-scale flows meandering across major bathymetric obstacles is a result of the conservation of potential vorticity (f/h , where f is the Coriolis factor and h is the bottom depth for a barotropic flow such as the Southern Ocean; Marshall 1995). To conserve its potential vorticity over a shallowing topography, an eastward flow such as the ACC deviates equatorwards, while it bends back polewards after crossing the topographic obstacle. Such northward deviations of the southern ACC flows across the Scotia Arc and the Kerguelen Plateau results in the influx of cold waters into the areas close to the islands, which may further increase nutrient input and therefore biological productivity (Ward et al. 2002).

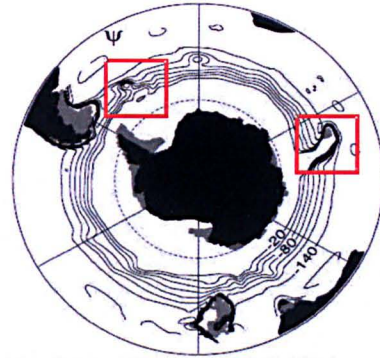


Figure 2.4: Mass streamfunction (S_v) of fluid parcels of the ACC negotiating a variable bottom topography while conserving potential voracity, showing the northward deviation of the ACC flow in the Scotia Sea and at the Kerguelen Plateau. Figure from Marshall (1994) and Rintoul et al. (2001).

Locations downstream of intense ACC bathymetric steering are further characterized by intensification of the PF (in terms of increased cross-frontal widths and temperature gradients), decreased large-scale frontal meandering, but increased mesoscale activity and eddy formation (Moore et al. 1999b; Sallée et al. 2008). The Scotia Sea and Kerguelen Plateau are among the regions where these effects are the strongest in the Southern Ocean due to the strong bathymetric steering of the ACC (Moore et al. 1999b). Mesoscale features such as eddies have been shown to be locations of increased biological productivity and biomass accumulation (Rodhouse et al. 1996; Pakhomov & Froneman 2000; Nel et al. 2001; Strass et al. 2002; Dragon et al. 2010), and may therefore increase structuring and predictability in patterns of biological activity in the ocean. The prominent

steering effect of the rugged bathymetry of the Scotia Sea and of the extended Kerguelen Plateau further increases the stability of oceanographic features in these areas. In the Scotia Sea, the frontal jets are more variable and more widely spread out than in the Drake Passage, but still form a series of intense currents navigating through narrow deep channels formed by complex bottom topography (Orsi et al. 1995; Belkin & Gordon 1996; Sokolov & Rintoul 2009). Eddies of apparent high spatial stability have been identified in the area to the north of South Georgia associated with bathymetric features in the flow of the PF and SACCF (Rodhouse et al. 1996; Trathan et al. 1997; Trathan et al. 2000; Thorpe et al. 2002b; Meredith et al. 2003a; Meredith et al. 2005), which have been reported to be explored by foraging albatrosses and king penguins (Rodhouse et al. 1996; Trathan et al. 2008; Scheffer et al. 2010; Scheffer et al. 2012). In the area to the south-east of Kerguelen, the immediate effects of the pronounced Kerguelen Plateau bathymetry lead to persistent patterns of flow channelling and upwellings along the south-eastern shelf break of the Kerguelen Plateau (Park et al. 1998; Park et al. 2008b; Roquet et al. 2009; Park & Vivier 2011), which have been reported to be utilised by foraging king penguins and other marine predators (Charrassin et al. 2004; Hindell et al. 2011).

Overall, the islands of South Georgia and Kerguelen appear to provide for favourable conditions for many breeding marine predators, being characterized by the presence of several frontal zones in proximity of the breeding colonies and by increased biological productivity through bathymetry-related upwellings as well as the intensification of ACC fronts and mesoscale activity. Stability in larger-scale frontal patterns through upstream bathymetric steering, and of mesoscale features through local bathymetry may lead to high levels of structuring and predictability of such biological resources in proximity of the islands, therewith increasing the profitability of the Scotia Sea and Kerguelen Plateau for foraging marine predators.

However, local oceanography and the location of the islands in relation to the different ACC frontal zones show important differences. In order to better understand the foraging behaviour of diving marine predators such as king penguins and to compare behavioural patterns at both study locations, it is necessary to have knowledge about detailed oceanographic patterns at both study locations at the surface and at depth.

2.1.1. Oceanography in the Scotia Sea and in the area to the north of South Georgia

South Georgia is situated within the Antarctic Circumpolar Current (ACC) flow in the Scotia Sea part of the southwest Atlantic Ocean, with the Polar Front (PF) to the north and the Southern ACC Front (SACCF) close to the island. Upstream of the Scotia Sea, the ACC fronts are channelled at their narrowest meridional constriction within Drake Passage and then diverge as the ACC enters the Scotia Sea (Orsi et al. 1995; Brandon et al. 2004). In the Scotia Sea, the Scotia Arc rises from depths of 3000 – 5000 m as a chain of islands from the Antarctic Peninsula to the tip of South America. It represents one of the major

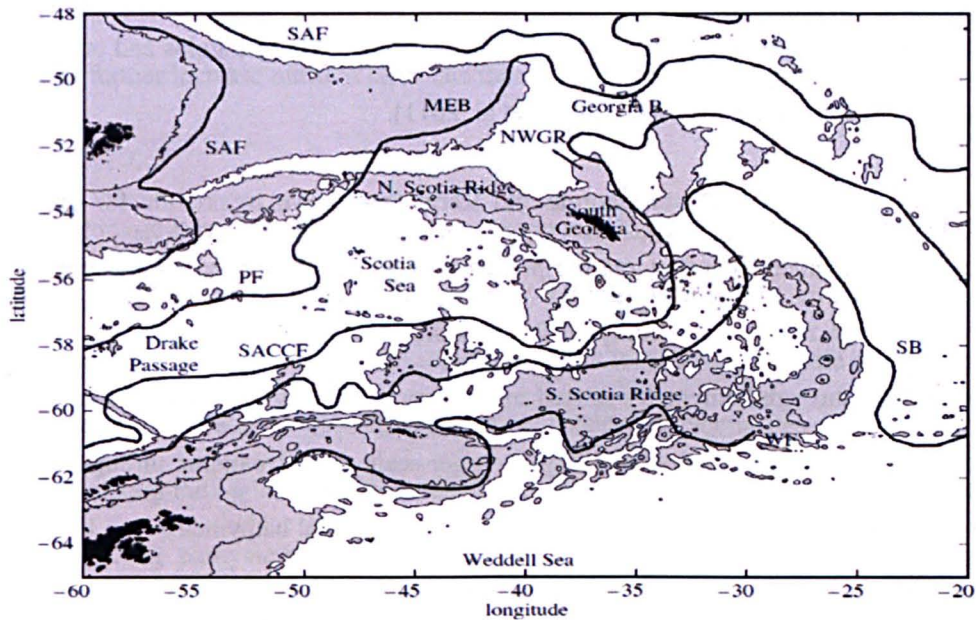


Figure 2.5: Oceanography and bathymetry of the Scotia Sea. ACC fronts are shown in black, bathymetry in grey shades. SAF: SubAntarctic Front; PF: Polar Front; SACCF: Southern ACC front; SB: southern ACC boundary. NWGR: North West Scotia Rise; MEB: Maurice Ewing Bank. Figure from Murphy et al. (2007).

bathymetric obstacles in the path of the ACC, significantly deviating the frontal flows to the north (Marshall et al. 1995; Orsi et al. 1995; Moore et al. 1999b). Much of the central abyssal plain of the Scotia Sea is 3000 – 4000 m deep, with pronounced submarine structures and seamounts such as the North West Georgia Rise (NWGR), the North East Georgia Rise (NEGR) and the Maurice Ewing Bank (MEB) in the area to the north of South Georgia. The combination of strong flow and mixing in an area of rugged bathymetry makes the Scotia Sea one of the most physically energetic regions of the Southern Ocean (Murphy et al. 2007b). The rugged bathymetry of the Scotia Sea plays an important role in determining the ACC frontal paths, but also for circulation patterns in the inter-frontal zones.

In contrast to most other king penguin breeding colonies which are located north of the PF (Bost et al. 2009), South Georgia is situated south of the PF. The PF deviates northward after exiting the Drake Passage and crosses the complex bathymetry of the North Scotia Ridge and passes over the southern edge of the MEB (Trathan et al. 1997; Trathan et al. 2000; Moore et al. 1999b). Recurrent warm-core rings presumably related to bathymetric features have been reported within the PF flow in the area to the north of South Georgia to the east of the MEB and on the north-eastern tip of the NEGR (Trathan et al. 1997; Trathan et al. 2000; Rodhouse et al. 1996; Scheffer et al. 2010).

The flow regime close to South Georgia is dominated by the SACCF, which is deflected northward by the South Scotia Ridge and loops anticyclonically around the South Georgia peri-insular shelf before retroflecting north of the island (Orsi et al. 1995, Thorpe et al. 2002b, Meredith et al. 2003a; Boehme et al. 2008a)

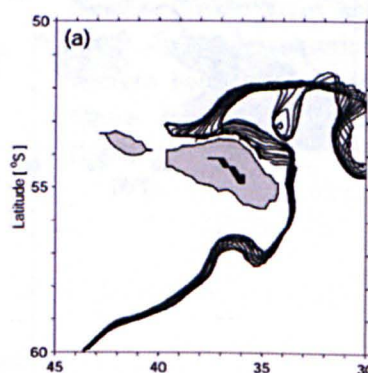


Figure 2.6: Path of the SACCF in the Scotia Sea, showing the presence of an eddy to the north of South Georgia. Figure from Thorpe et al. (2002).

at $\sim 36^\circ\text{W}$. The SACCF flow is rich in nutrients (Ward et al. 2002), and hosts a high biomass of zooplankton (Murphy et al. 2004). The Antarctic Zone (AAZ) is situated between the PF and the SACCF; it is characterized by the meeting of cold Antarctic waters and warmer surface waters from the PF. A complex eddy field has been described in the AAZ north of South Georgia as well as a warm-core anticyclonic circulation at around 52°S , 35°W (Thorpe et al. 2002b; Meredith et al. 2003b).

Vertical sections across the SACCF flow to the north of South Georgia show cold Winter Water (WW) layers centered around 100-150 m depth (Ward et al. 2002; Brandon et al. 2004), as well as doming of isopycnals associated with the SACCF flux (Ward et al. 2002). Such isopycnal doming appears to result in the presence of Circumpolar Deep Water (CDW) at depths <250 m in some locations close to the northern shelf break of South Georgia (Brandon et al. 1999; Brandon et al. 2004; Thorpe et al. 2002b; Ward et al. 2002; Ward et al. 2012).

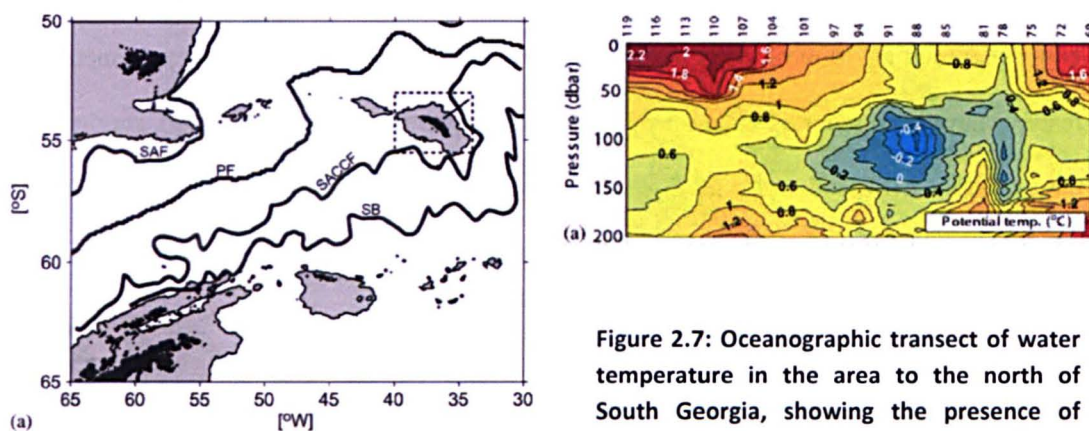


Figure 2.7: Oceanographic transect of water temperature in the area to the north of South Georgia, showing the presence of cold-water layers between 100-200 m depth, and local isopycnal doming associated with the SACCF flux. Figure from Ward et al. (2002).

2.1.2 Oceanography over and around the Kerguelen Plateau

The Kerguelen archipelago is located within the flow of the Antarctic Circumpolar Current (ACC) in the south Indian Ocean, with the Sub-Antarctic Front (SAF) situated to the north and the Polar Front (PF) and Fawn Trough Current (FTC) to the south. The Kerguelen Plateau is a major bathymetric feature of the Southern Ocean, significantly altering the flow of the ACC, including the deeper ACC flow (Park et al. 1998; Park et al. 2008b; Sokolov & Rintoul 2009; Park & Vivier 2011). To the southwest of the Kerguelen Plateau, the PF and the FTC are separated by a distance of up to eight degrees of latitude, but they are steered by the local topography of the Kerguelen shelf and finally closer together close to the outlet of the Fawn Trough in the Australian-Antarctic Basin (52°S, 82°E) (Park et al. 2008b). The juxtaposition of these flows of different origin and with different properties creates a dynamic zone characterized by enhanced mixing and strong gradients, which in turn enhances biological productivity (Lima et al. 2002; Thomas & Emery 1988). Iron enrichment by the island mass effect further increases production in the waters downstream of the Kerguelen Plateau (Blain et al. 2001; Blain et al. 2007).

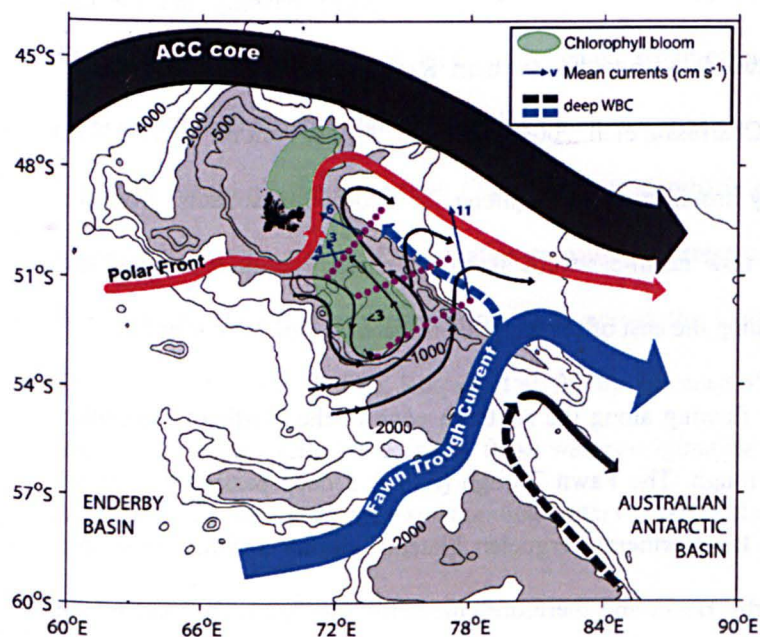


Figure 2.8: Schema of the general circulation over and around the Kerguelen Plateau. Discontinuous bold lines indicate subsurface western boundary currents. Figure from Park et al. (2008).

The Northern Kerguelen Plateau is characterized by a complex topography (Park et al. 2008b Fig.2.9), which significantly impacts the local circulation (Park et al. 2008b; Roquet et al. 2009; van Wijk et al. 2010; Park & Vivier 2011). There are differing opinions in the literature concerning the exact frontal pathways over the Kerguelen Plateau (Orsi et al. 1995; Belkin & Gordon 1996; Park et al. 2008b; Park & Vivier 2011; Roquet et al. 2009; Sokolov & Rintoul 2009; van Wijk et al. 2010), mostly due to the complex interaction of oceanography with the bathymetry of the Kerguelen Plateau and the use of different criteria (SST, SSH, SST gradients, Chl-a, subsurface characteristics) and threshold values for frontal definition.

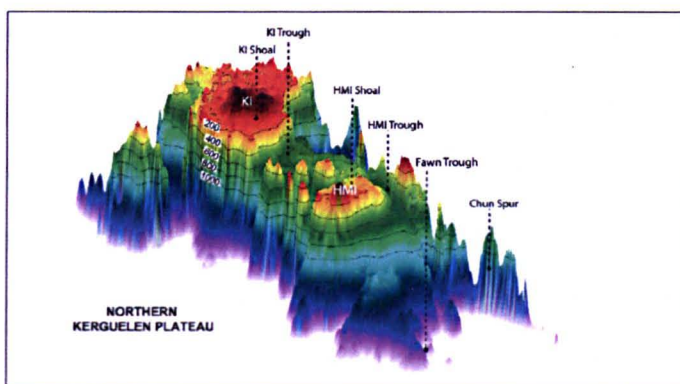


Figure 2.9: 3D view of the complex bathymetry for depths shallower than 2000m over the Northern Kerguelen Plateau. Figure from Park et al. (2008). KI: Kerguelen Islands, HMI: Heard/McDonald Islands.

Most recently the PF has been identified to flow eastwards across the northern Kerguelen Plateau just south of Kerguelen (Park et al. 1998; Charrassin et al. 2004; Park et al. 2008b, Park & Vivier 2011). It then flows anticyclonically around the island (along the 200-500m isobaths) from the south-east and continues its flow north-eastward along the eastern continental shelf and then again south-eastwards along the east of the Kerguelen Plateau (Park & Vivier 2011).

The FTC is a strong current flowing along the southern edge of the Northern Kerguelen Plateau through the Fawn Trough. The Fawn Trough (FT) is a deep passage (<2800m) separating the Southern and the Northern Kerguelen Plateau, joining different separated flows of the upstream Enderby Basin and therefore channelling an important part of the ACC flow (Park et al. 2008b; Roquet et al. 2009). The FTC has been assigned to different

ACC fronts based on altimetry (SACCF: Park et al. 2008b; Park & Vivier 2011; SPF: van Wijk et al. 2010). For simplicity we refer to the flow passing the Fawn Trough as the Fawn Trough Current (Roquet et al. 2009), and will comment on frontal patterns later in the discussion. Despite differences in the interpretation of surface signatures, based on subsurface signatures the FTC is characterized by the northern limit of Winter Water (WW), corresponding to the subsurface temperature minimum (T_{\min}) of 0°C situated at around 100 m depth (Roquet et al. 2010), and the southern limit of Upper Circumpolar Deep Water (UCDW), corresponding to the mid-depth temperature maximum (T_{\max}) of 2°C (Roquet et al. 2010; van Wijk et al. 2010; Park & Vivier 2011).

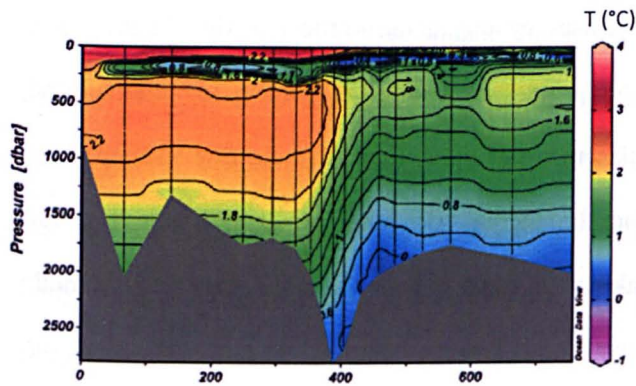


Figure 2.10: Temperature section across the Fawn Trough from Heard Island to the Southern Kerguelen Plateau along a south-easterly transect. WW can be identified by the 0°C isotherms, UCDW by the 2°C isotherms at greater depths. Figure modified from Roquet et al. (2010).

Flowing east from the Fawn

Trough passage, most of the FTC is deflected south-eastwards by the Chun Spur, a pronounced bathymetric feature at the south-eastern end of the Kerguelen Plateau. However, while all the deep flow (T_{\max} , ~ 400 m depth) is deviated to the south by the Chun Spur barrier, a part of the shallower waters (corresponding to the T_{\min} layer, cold WW, ~ 100 m depth) is advected northwards across the Chun Spur to the south-east of Kerguelen (Park et al. 2008b; Roquet et al. 2010). Because of its unique characteristics of cold waters of Antarctic Zone origin, these waters originating from the FTC can be clearly distinguished from the warmer surrounding waters (Roquet et al. 2010).

The cold WW advected from the Fawn Trough over the Chun Spur flows northwards along the eastern shelf break of the Kerguelen Plateau, forming a cold-water subsurface tongue that can extend up to the latitude of Kerguelen (Charrassin et al. 2004; Park et al. 2008b; van Wijk et al. 2010), where it reaches depths of ~100 m (Charrassin et al. 2004). Its northward extension appears to be variable, but the factors affecting the flow are not well understood.

The northern Kerguelen Plateau to the south of Kerguelen is characterized by relatively weak currents between the PF and the FTC (Park et al. 2008b; Park & Vivier 2011). Internal tides, generated by the interaction of tidal currents and slope bathymetry, play an important role for oceanographic processes by enhancing vertical mixing in the water column (Park et al. 2008a). These internal tides are of high frequency (semidiurnal) and highly non-linear, with isopycnal displacements of up to 80 m at depths of 80-200 m (Park et al. 2008a). Turbulence resulting from the internal tides is the principal driving force for elevated vertical mixing and iron uptake in the water column (Mongin et al. 2008; Maraldi et al. 2009). The high frequency and non-linearity of the internal tides makes the area over the plateau to the south of Kerguelen highly dynamic. Due to the enhanced mixing and upward transfer of iron in the water column from the internal tides, the area over the northern Kerguelen Plateau is characterized by high primary productivity in comparison with surrounding areas (Mongin et al. 2008; Park et al. 2008b). These enhanced and spatially restricted sources of primary production have important implications for the regional marine foodweb, including predators (Park & Vivier 2011) such as king penguins.

2.2 The king penguin (*Aptenodytes patagonicus*)

Penguins are a distinctive group of flightless, long-lived pelagic seabirds. The penguin family (Spheniscidae) consists of 18 existing species (Williams 1995), but 16 to 19 according to some authors. Penguins only occur in the Southern Hemisphere, where they show a wide distribution from the Equator to the Antarctic continent. In most breeding locations penguins form large colonies of several thousands up to hundreds of thousands of pairs during the breeding season between Austral spring and autumn (approximately November - March).

Penguins are well adapted to their aquatic life, with a streamlined body and wings that are used as flippers. In contrary to other diving seabirds, penguins have lost their flight capacity. Their adaptation to aquatic life is therefore not constrained by flight adaptations, and various physiological characteristics make them excellent divers. The streamlined body reduces drag, and the wings evolved into flippers allow efficient underwater propulsion. Solid, dense bones increase the body density and help to overcome buoyancy when diving. The relatively short feet are pressed against the tail to aid steering while moving under water (Williams 1995) and are not used for propulsion as in some species such as cormorants and shags (Sato et al. 2007).

During the breeding period, the individuals within a breeding pair alternate foraging trips at sea with periods on land when they engage in incubation or chick guarding activities. The penguins' foraging behaviour at sea, particularly during the breeding season, when they are normally unobservable, can be studied by equipping individuals with micro-electronic devices that record different activity patterns. Such devices are generally deployed just before the birds departure to sea, and recovered after its return to the colony.

The king penguin (*Aptenodytes patagonicus*, Miller 1778) is the second largest penguin after the emperor penguin. Adults are 85 - 95 cm tall and weigh 12 - 16 kg, with anatomical characteristics varying among breeding locations. King penguins breed on many of the sub-Antarctic islands between 45°S and 55°S within a distance of 400 km of the Antarctic Polar Front (PF) (Bost et al. 2012). Current estimates of their world population suggest ~1,600,000 breeding pairs; however these numbers are thought to be underestimated as most counts only include successful breeders in January and do not generally include failed or late-nesting pairs (Bost et al. 2012). The largest breeding populations are still on Crozet Island with around 612,000 – 736,000 pairs (corresponding to about 50% of the global population), ~342,000 on the Kerguelen Islands, ~ 450,000 on South Georgia Island, 150,000 – 170,000 on Macquarie Island and ~80,000 on Heard Island (see review in Bost et al. 2012). These large numbers make king penguins an important component of the Southern Ocean foodweb (Woehler 1995). There are two subspecies recognised; *Aptenodytes patagonicus patagonicus* which breeds in the south Atlantic and *Aptenodytes patagonicus halli* which breeds in the Southern Indian Ocean.

South Georgia and Kerguelen are two of the main breeding locations for king penguins (Woehler 1995; see Bost et al. 2012). Our study was carried out at the Hound Bay colony on the north coast of South Georgia (54°23'S, 36°15'W), and at the Ratmanoff colony on the east coast of Kerguelen (49°14'S, 70°33'E).



Figure 2.11: The Ratmanoff king penguin breeding colony at Kerguelen.

Breeding cycle:

Like many other seabirds, king penguins are long-lived, lay one egg during each breeding cycle and take months to rear their chicks. The king penguins' breeding cycle extends over more than one year (14-15 months), which is the longest among seabirds (Weimerskirch et al. 1992, see Fig. 2.13). After a moulting period of around 22 days on land, the penguins have to replenish their energy reserves at sea before starting reproduction. The first adults arrive at the colony to breed in early November. After courtship and egg-laying, the female goes to sea to feed, leaving the male in charge of the first incubation shift. The male stays fasting on the egg without food for approximately 21 days, when the female returns to the colony to take her turn incubating the egg. The chick hatches after approximately 54 days

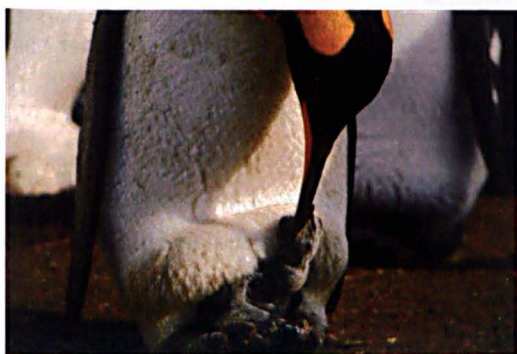


Figure 2.12: A king penguin couple during incubation at the moment of the exchange of the egg, and the hatched chick still on the feet of the adult.

of incubation (Stonehouse 1960). During incubation and the early phases of chick-rearing, the parents take turns to incubate the egg or brood the young chick on their feet, thus undergoing prolonged periods of fasting ashore while the partner is foraging at sea (Stonehouse 1960; Groscolas 1990). Hatching usually occurs from mid-January to February, both parents alternate brooding duties and foraging trips of 4-12 days. After about one month around mid-February, the chicks covered in down are thermally emancipated and group into crèches. Both parents then resume foraging trips to

provide their growing offspring with food. By the end of Austral summer (mid-April), the almost fully grown chicks have gained substantial fat reserves (Cherel et al. 1993) to

overcome the fasting period during austral winter. During Austral winter (May - September), the adults desert the colonies for extended period (Weimerskirch et al. 1992) and forage in areas further south near the pack-ice (Charrassin & Bost 2001; Bost et al. 2004) due to the scarcity of prey in the areas around their breeding colonies (Charrassin & Bost 2001). If the chick survives the long fasting period during winter (up to five months of fasting, Cherel et al. 1987), the parents return to chick-feeding by mid-September with recovery of chick growth until fledging around mid-November. Parents then have to undergo moulting before they breed again.

Raising a king penguin chick usually takes 10 to 13 months. This results in the inability to breed successfully every year. Thus the breeding cycle is asynchronous in king penguins (Olsson 1996; Weimerskirch et al. 1992), where successfully reproducing birds can only start to breed late in the subsequent year due to the long time necessary to fledge a chick, moult and recover sufficient body reserves for on-land fasting. This usually allows the adults to raise only 1 chick every other year (Weimerskirch et al. 1992).

During the breeding season, king penguins undergo important energy constraints, as the continuous presence of one adult is required on land with the egg/chick, and the other has to forage at sea. Penguins therefore acquire large body reserves prior to their arrival on land for breeding (Weimerskirch et al. 1992; Cherel et al. 1993; Gauthier-Clerc et al. 2001). Insufficient body reserves may induce or result in complete breeding failure, where parents may sometimes abandon their egg or chick and return to forage at sea before their partner's return to the colony (Olsson 1997; Groscolas et al. 2000; Gauthier-Clerc et al. 2001; Olsson & van der Jeugd 2002).

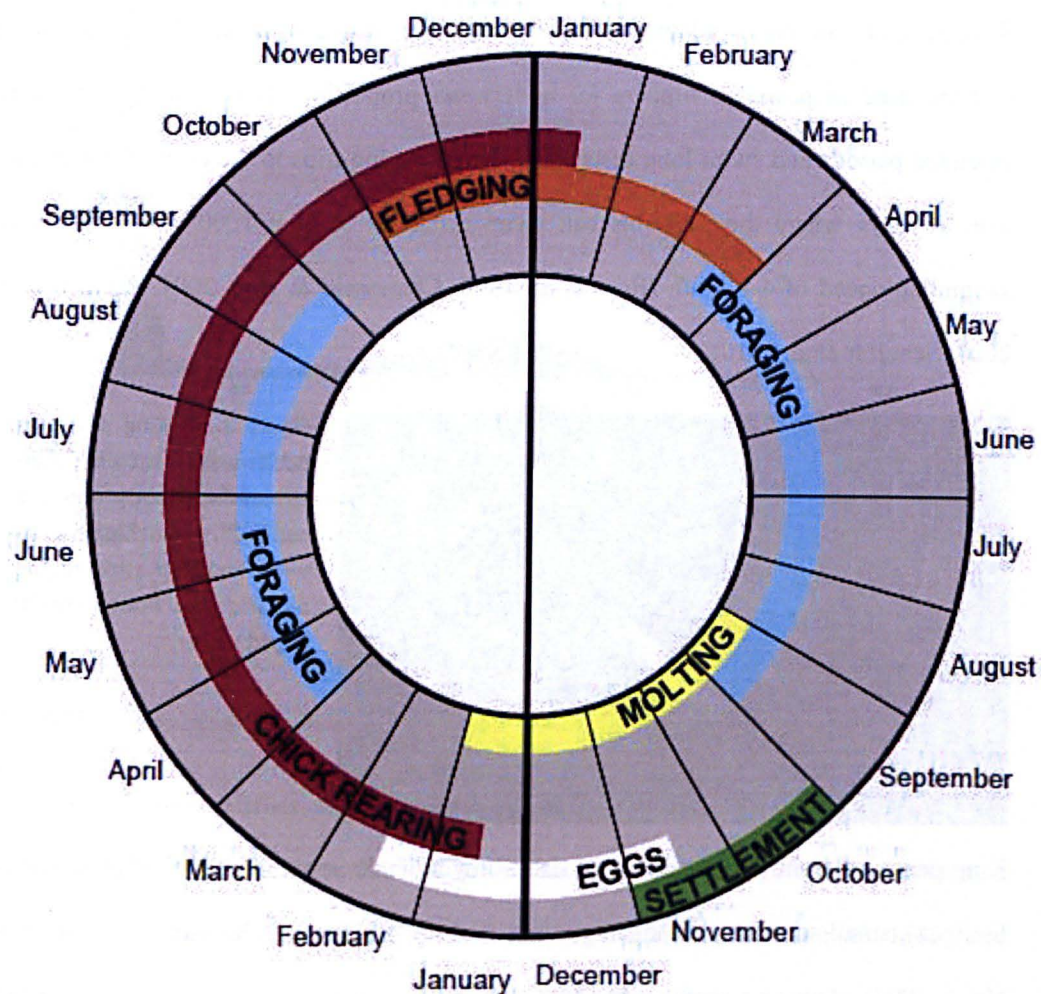


Figure 2.13: King penguins breeding cycle, showing the asymmetry in the different periods of reproductive and foraging activities over the course of two years. Figure from Bost et al. (2012).

Foraging ecology: Prey and at-sea behaviour:

King penguins are highly adapted to their oceanic life, with a streamlined body and wings that are used as powerful flippers for underwater propulsion. They can stay at sea for extended periods and swim long distances. Their foraging trips to the Polar Front can last over 20 days where the penguins can swim distances of over 1000 km with a mean swimming speed of 4-7 km/h (Bost et al. 1997; Charrassin & Bost 2001; Trathan et al. 2008; Scheffer et al. 2010).



Figure 2.14: King penguins under water, showing their streamlined body and the use of their flippers as wings in adaptation to the aquatic life. Photo credit: Ingrid Visser.

King penguins mainly feed on lantern fish or myctophids (more than 90% of their diet per biomass), small schooling mesopelagic fish, and squid (Cherel & Ridoux 1992; Olsson & North 1997). Among penguins, the two *Aptenodytes* species, the emperor and the king penguin, are the best divers in terms of depth and duration. King penguins can dive to depths of more than 350 m (Kooyman et al. 1992; Pütz et al. 1998; Charrassin et al. 1998, 1999; Charrassin & Bost 2001; Bost et al. 2007). Mean foraging depths are between 100 – 200 m, increasing between incubating and creching (Charrassin et al. 2002) and during winter (Moore et al. 1999a).

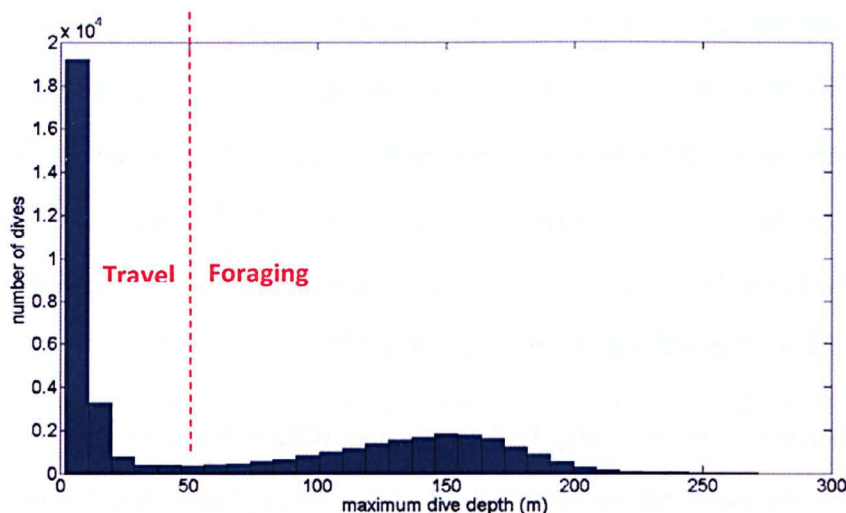


Figure 2.15: Histogram of the maximum dive depths of king penguins, showing the bimodal distribution of shallow travel dives (0-50m depth) and foraging dives (>50m depth). Dive data used are from 8 king penguins randomly selected from the dataset used in this thesis (1 penguin/year).

Myctophids, king penguins' main prey

Myctophids, or lanternfishes, are small mesopelagic fish of the large family Myctophidae, and are found in the oceans worldwide. In the Southern Ocean, myctophids represent a major biomass resource (estimated 70 – 200 million tonnes, Lubimova et al. 1987) and food resource for a variety of marine predators, providing for an important alternative trophic pathway to the more commonly discussed krill-based system (Perissinotto & McQuaid 1992; Georges et al. 2000).

Despite their ecological importance, data on the distribution and ecology of Southern Ocean myctophids are relatively scarce (Collins et al. 2008). Oceanographic patterns appear to play an important role in the distribution of myctophids, as they are generally associated with particular water masses or temperature ranges (Hulley 1981, Kozlov et al. 1991, Collins et al. 2012, Fielding et al. 2012), as well as with fronts and related oceanographic features (Brandt et al. 1981, Kozlov et al. 1991, Pakhomov et al. 1996, Rodhouse et al.

1996). Strong thermal gradients such as the thermocline appear to represent particularly favourable conditions for myctophid to aggregate (Brandt et al. 1981, Kozlov et al. 1991). The occurrence of strong thermal gradients at shallow depths is therefore thought to lead to dense and shallow myctophid aggregations at the Polar Front (PF), particularly during dusk and dawn when king penguins are able to exploit shallow myctophid resources before their descent to greater depths during daytime (Bost et al. 2002).

Myctophids represent the main prey for king penguins (Cherel & Ridoux 1991; Olsson & North 1997). The horizontal and vertical distribution of myctophids is therefore thought to play a key role in the foraging behaviour of king penguins (Bost et al. 2002). However, detailed information about the distribution of myctophid as well as the composition of king penguin diet (different myctophid species, squid) is scarce, and varies between locations. Therefore, some statements concerning king penguins diet and/or foraging behaviour in relation to the distribution of myctophids in the watercolumn remain partly speculative.

Population development and potential threats:

King penguin populations have been increasing since the 1970's (Weimerskirch et al. 1992; see review in Bost et al. 2012) after strong population declines in the 19th and early 20th century due to the rendering of birds for their oil to fuel the boilers during the sealing industry. King penguin populations are now increasing or have stabilized at all breeding colonies, and the species has been listed in the Least Concern category on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2011).

However, possible change in the availability of their main prey resulting from environmental change is one of the main threats to king penguins (Bost et al. 2012). Warming sea surface temperatures in the penguins' foraging areas leading to decreases in

sea-ice extent and southward shifts of the PF, one of the main foraging areas of king penguins during summer (Bost et al. 1997; Guinet et al. 1997; Charrassin & Bost 2001; Bost et al. 2009a), is thought to significantly impact the distribution of king penguins' prey and therewith the bird's foraging behaviour and success, and ultimately their population development (Le Bohec et al. 2008; Péron et al. 2012). However, such impacts of changes in prey availability from environmental change may not only be negative, but may also represent future opportunities of better access to prey resources for king penguins in some locations.

2.3 Tracking of king penguins foraging behaviour:

At-sea movements of king penguins were followed using ARGOS (PTT Telonics St10; PTT Sirtrack Kiwisat 101) and Global Positioning System (GPS: Navsys Track-Tag; Sirtrack Fastloc) tracking for analyzing their movements at the sea surface, and Time-Depth-Temperature-Recorders (TDR, Mk7 and Mk9 devices) for tracking their dive behaviour. Combining observed penguin behaviour with oceanographic data at the surface and at depth allowed me to explore how animals adjust their horizontal and vertical movements in response to their environment. The size of tracking devices has significantly reduced over the past few years, allowing for fine-scale tracking of animals with a minimal effect on their behaviour (see Ropert-Coudert & Wilson 2005; Hooker et al. 2007).

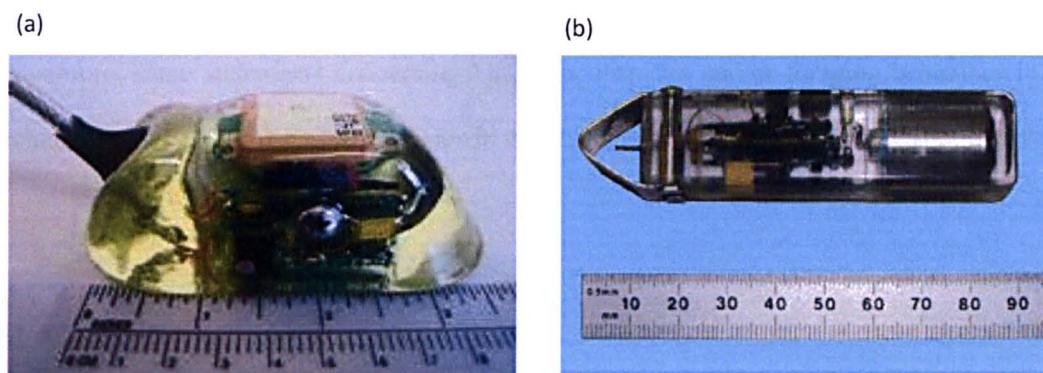


Figure 2.16: Tracking devices for penguins surface and underwater movements.

(a) A Fastloc GPS device.

(b) A Mk9 TDR device with external fast-responding temperature sensor.

Tracking of king penguins was carried out during the breeding period during the Austral summer between December and February, following birds during their incubation and broodguard foraging trips. Birds were selected in the colony during the exchange of the egg between the return of one adult to the colony and the departure of their partner. The departing birds were then captured after they had left the colony but before they entered the sea. Devices were attached using methods modified from Wilson et al. 1997. Briefly,

devices were attached using quick-drying two-part glue and waterproof Tesa tape. To aid the recovery of devices, all birds were marked on their front with coloured hair dye. After the birds returned from a single foraging trip, the devices were recovered.

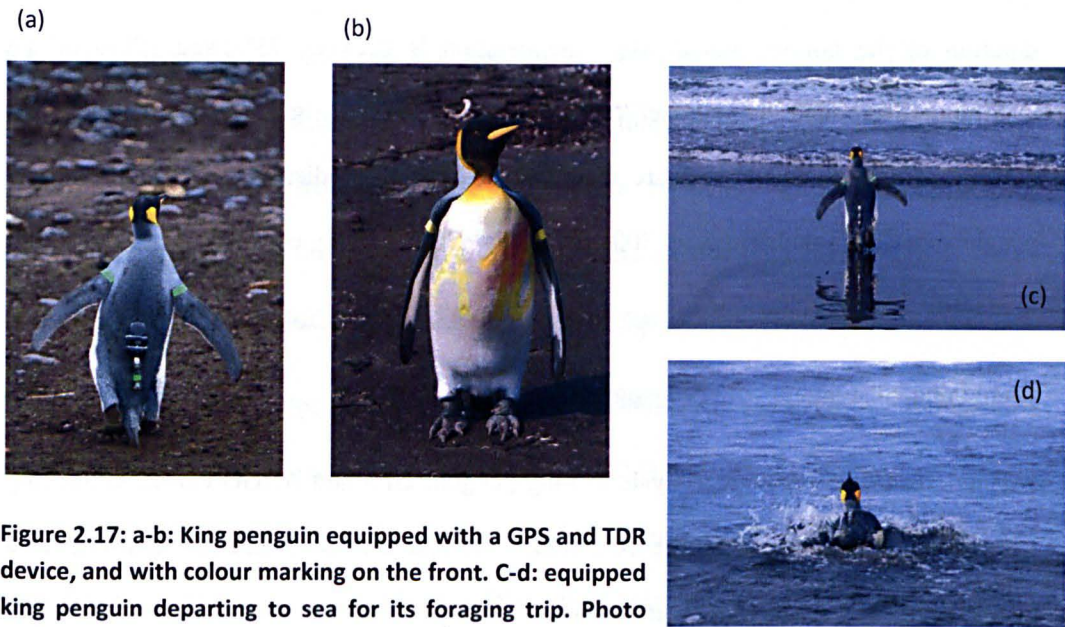


Figure 2.17: a-b: King penguin equipped with a GPS and TDR device, and with colour marking on the front. C-d: equipped king penguin departing to sea for its foraging trip. Photo credits: Alex Chevallier.

Analysis of surface and diving data:

Surface movements from satellite and GPS tracking data was analysed using foraging trip parameters such as total distance and duration of the trip as well as maximum distance from the colony as indicators of the total foraging trip effort. Furthermore I used the degree of straightness of a foraging trip as a measure of the directedness of foraging to a particular location (straightness index). To analyse changes in surface movements I considered the rate of turning in the foraging track as an indicator for search effort for prey at different scales. I used First Passage Time analysis (Fauchald & Tveraa 2003), which is a current index for the quantification of animals search behaviour. Based on this method, behavioural states of travel or search behaviour were assigned to each at-sea location of the penguins.

Analysis of diving behaviour throughout the foraging trip was based on the TDR data. Dive parameters that are thought to be reliable indicators for characterising dive behaviour (e.g. Kooyman et al. 1992; Pütz & Cherel 2005) were investigated and related to the horizontal tracking data. These dive parameters were maximum dive depth, dive duration, duration of the bottom period when the penguin is between 75% and 100% of the maximum depth and the number of bottom undulations (wiggles). Bottom time and number of bottom undulations are thought to be reliable indicators for feeding among penguin species (Takahashi et al. 2004; Bost et al. 2007, Halsey et al. 2007), and was used to identify feeding behaviour.

Combining behavioural with oceanographic data:

I undertook a simultaneous analysis of king penguin GPS and ARGOS satellite tracking data and time-depth-temperature recordings overlaid on environmental datasets. This integrated approach allowed a detailed visualisation of penguin movements and activities in the three dimensions of their habitat. The environmental datasets of water temperature, sea surface height and bathymetry were combined to create a detailed 3-dimensional image of the environmental conditions in the foraging areas, and to identify oceanographic structures within the foraging area of tracked animals. Finally I overlaid the penguin behavioural recordings on the environmental images in order to identify most favourable foraging conditions with regards to oceanographic features at the surface and at depth.

For the characterization of the marine environment used by the penguins during their foraging trips I used a combination of remote-sensing and in-situ data. Remote-sensing technologies record environmental data in high resolution through satellites and allow continuous monitoring of environmental conditions even in remote or inaccessible areas. To characterize oceanographic conditions at the surface and identify distinct features in the

foraging area of king penguins, I used Sea Surface Temperature (SST), Sea Surface Height (SSH) as well as geostrophic velocity data.

SST data: SST data characterizes the ocean temperature at its surface. For the analysis of tracking data in relation to SST I used OSTIA (Operational Sea Surface Temperature and Sea Ice Analysis) SST data from The Met Office (FitzRoy Road, Exeter, UK). OSTIA provides gap-free foundation SST values, SST_{nd}, defined as the temperature of the water column at the surface free of diurnal temperature variability (daytime warming or nocturnal cooling) from interpolation of satellite and in-situ data. More details about OSTIA are available at http://ghrsst-pp.metoffice.com/pages/latest_analysis/ostia.html.

SSH and geostrophic velocities: Sea Surface Height (SSH) is the height of the ocean's surface compared to an accepted reference height. SSH reflects the strength of oceanic currents and gradients, and makes oceanographic features such as thermal fronts and eddies clearly apparent. Geostrophic velocities characterize the gradient in SSH, indicating the strength and direction of an ocean current. SSH and geostrophic velocities data provided by the AVISO altimetry satellites (<http://www.aviso.oceanobs.com/en/data/products/sea-surface-height-products/global/madt/index.html>) were used.

Bathymetry data: Bathymetry characterizes the relief of the ocean floor. This parameter is important as it plays an important role in oceanographic processes such as conditioning the flows of ocean currents, and impacting vertical processes such as upwellings. In this study I used the Smith and Sandwell Global Seafloor Topography from Satellite Altimetry and Ship Depth Soundings (NOAA and Scripps Institution of Oceanography) (Smith & Sandwell 1997). More details for the dataset are available at http://gcmd.nasa.gov/records/GCMD_SIO_NOAA_SEAFLOORTOPO.html.

Vertical temperature data:

Vertical temperature values were obtained from the external TDR Mk9 sensor data. TDR Mk9 temperature sensors provide high quality data (accuracy $0.1^{\circ}\text{C} \pm 0.05^{\circ}\text{C}$, Simmons et al. 2009), and were therefore used for determining the properties of the water column encountered during penguin dives. For each dive, temperature data that were recorded during the descent and ascent phases were projected onto a vertical axis corresponding to the maximum depth of the dive and averaged at 1-m depth intervals. This resulted in regularly gridded temperature data in the vertical plane, and facilitated calculation of the average potential differences in the water column properties encountered during the descent and ascent phases due to horizontal movements of the penguins. A 5m moving average filter was then applied to the temperature profiles, allowing for correction of any potential measurement errors from the TDR temperature sensors without smoothing out thermal discontinuities in the water column. To compensate for the surface heating effect by direct sun exposure and penguin body temperature on the temperature sensors (McCafferty et al. 2007), temperature values collected between 0 and 10 m were replaced by the value measured at 10 m depth during the ascent. Based on the regularly gridded temperature profiles I calculated the vertical water temperature gradient for each depth point; this was estimated as the temperature difference between 25 m above and 25 m below the given depth point (temperature gradient depth window based on visual inspection of dive-temperature profiles). Temperature gradients near to the depth extremes of a dive were calculated using the maximal depth range possible (limited by the surface for points $<25\text{ m}$ depth, and by the maximal dive depth for points $>\text{maximum depth}-25\text{ m}$). The resulting possible bias in gradient values may only impact the depth range between the maximum depth range of a dive and 25 m above, as dives shallower than 50 m were not considered for analyses of foraging behaviour. In my analyses, a temperature gradient of

+1 thus corresponds to a temperature increase of 1°C per 50 m depth, -1 to a temperature decrease of 1°C per 50 m.

The combination of the tracking and dive data allowed me to create a detailed 3-dimensional image of the king penguins activity in the ocean. The 3-dimensional environmental map containing water temperature, sea surface height and bathymetry allowed me to evaluate the penguins' behaviour in the context of the environmental conditions encountered during their foraging trips, and to identify key features of prey searching behaviour and feeding.

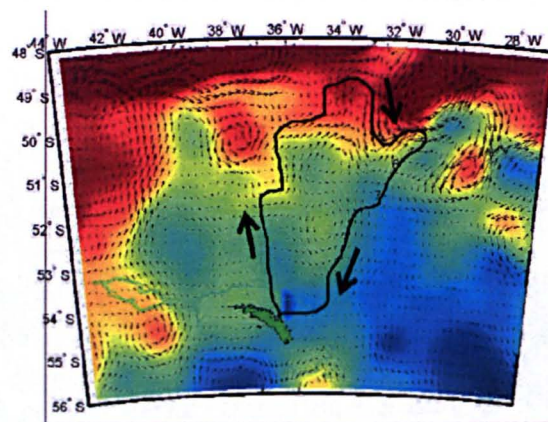


Figure 2.18: Horizontal movements of a king penguins' foraging trip overlaid on a map of remotely sensed Sea Surface Height and geostrophic velocities. Arrows indicate the travel direction of the tracked king penguin during its foraging trip.

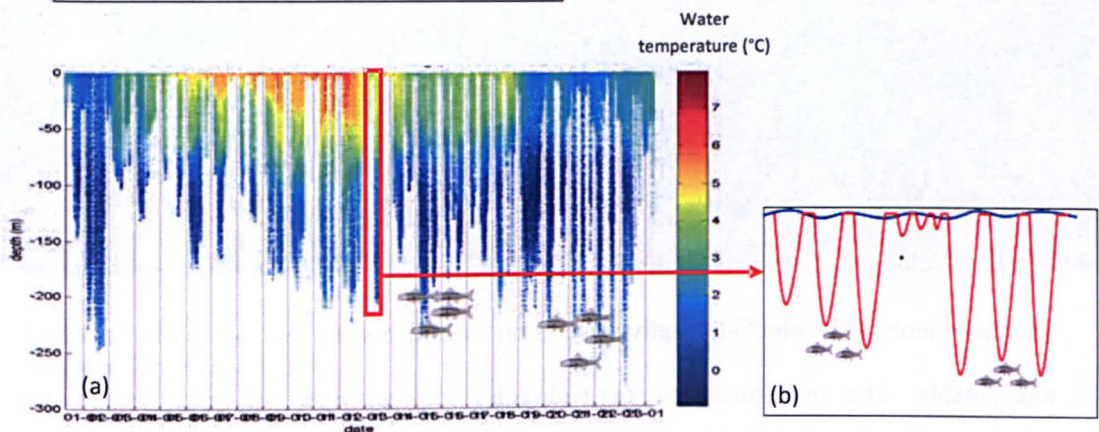


Figure 2.19: a - Depth-temperature profile of a king penguins' foraging trip recorded by a TDR device. Colour indicates the in-situ recorded water temperature. Depth and time allowed me to identify fine-scale movements of the penguin, indicating prey pursuit. b- Zoom into a dive profile, showing the individual dives (without temperature data, illustrating only the zoomed underwater movements). The putative position of prey are shown as an illustration.

Ethics and animal welfare in the context of field experiments in animal behaviour

Behavioural studies on animals such as the tracking of their movements have a central role in ecology and ethology. However, while carrying out any fieldwork or experiments on animals it is important to respect all animals, and to have consideration for their capacity of suffering and memory, and potential pain, distress or lasting harm. In some fields of scientific research on animal behaviour it is nevertheless necessary to use the animals where there is a reasonable expectation that the results will lead to a significant advance in knowledge or be of overall benefit for the animals. In this context the aim is to limit the use of animals for scientific purposes, trying to replace such methods whenever practical and to reduce the impact on the animals as much as possible.

The Scientific Committee on Antarctic Research (SCAR), an inter-disciplinary committee of the International Council for Science (ICSU) is charged with the initiation, development and coordination of international scientific research in the Antarctic. The ethical concerns about fieldwork on animals in Antarctica are covered by the SCAR Code of Conduct for the use of Animals for Scientific Purposes in Antarctica, which provides guidelines for researchers carrying out studies involving experiments on animals.

Biologging is a field where the use of animals is indispensable, and methods used have been recognized to have potential impacts on the animals. It is therefore important to conduct biologging fieldwork under strict consideration of the above issues, and ensure that procedures with potential negative effects on the animals are kept to a minimum where unavoidable. The miniaturization of biologging devices over the past decade has contributed to reduce the impact of such studies on the animals. All fieldwork involved in contributing to my thesis work was conducted under these guidelines, and ethical approval has been given by the BAS Ethics Review Committee (ERC).

Chapter 3

Foraging behaviour of king penguins breeding at South Georgia



Manuscript published in

Scheffer, A, Bost, CA, Trathan, PN (2012): Frontal zones, temperature gradient and depth characterize the foraging habitat of king penguins at South Georgia. *Marine Ecology Progress Series* 465, 281-297, doi: 10.3354/meps09884.

3.1 Abstract

Investigating the responses of marine predators to oceanographic structures is of key importance for understanding their foraging behaviour and reproductive success. Using Global Positioning System (GPS) and Time-Depth-Temperature-Recorder (TDR) tags, we investigated how king penguins breeding at South Georgia explore their foraging area over the summer season in both the horizontal and vertical dimensions. We determined how horizontal habitat use may relate to different Antarctic Circumpolar Current (ACC) frontal zones and associated thermal structuring of the water column. To study the penguins' use of the water column, we examined foraging niches defined by temperature, temperature gradient and depth, and explored the importance of these thermal properties for prey pursuit. King penguins foraged within the Polar Front (PF) and its southern edges during incubation, and the Antarctic Zone (AAZ) and Southern ACC Front (SACCF) during brooding. Foraging niches became more distinct with the advancing summer season, defined by strong thermal gradients at shallow depths in the AAZ, and weak gradients at greater depths in the SACCF. These niches indicate foraging in the sub-thermocline Winter Water (WW) in the AAZ, and in deep WW and Circumpolar Deep Water (CDW) at the SACCF. The influence of different ACC frontal zones in the area to the north of South Georgia appears to provide for a horizontally and vertically segregated environment. The presence of optional foraging areas and niches close to the colony clearly play an important role in these king penguins' foraging success.

3.2 Introduction

The behaviour and distribution of marine predators are generally thought to be determined by the location of their prey, but influenced by specific time and energy constraints. Prey distribution is strongly influenced by the structure of the marine environment (Owen 1981, Franks 1992), which is determined by physical properties such as temperature and temperature gradient. They govern the concentration of nutrients in the water column (Lima et al. 2002), which in turn influence the distribution and abundance of planktonic organisms and, hence, higher trophic levels including the prey of apex predators (Owen 1981, Lutjeharms et al. 1985, Schneider 1990). Surface features such as oceanographic fronts arise from where different water masses meet (Schneider 1990), and are, therefore, locations where different habitats as well as strong physical gradients occur in a spatially restricted area. Such a heterogeneous environment may be crucial for the existence of distinct foraging niches for predators.

King penguins are one of the most important avian consumers in the Southern Ocean (Woehler 1995). They feed mainly on myctophids (Cherel & Ridoux 1992, Olsson & North 1997), mesopelagic fish that are generally associated with particular water masses or temperature ranges (Hulley 1981, Kozlov et al. 1991, Collins et al. 2012, Fielding et al. 2012), as well as with fronts and related oceanographic features (Brandt et al. 1981, Kozlov et al. 1991, Pakhomov et al. 1996, Rodhouse et al. 1996). Among diving birds, king penguins are able to forage at depths of over 300 m (Charrassin et al. 2002), and are known to use thermal discontinuities for foraging (Charrassin & Bost 2001). However, we still have little detailed understanding about how these predators may explore the thermal structure of the water column in different marine environments, and how habitat use may be adjusted depending upon changing constraints.

King penguins experience changing time and energy constraints over the summer breeding season (Charrassin et al. 2002, Halsey et al. 2010). During incubation (December to February), each parent alternately incubates and then returns to sea to restore its body reserves in 2 to 3 week long foraging trips (Bost et al. 1997). After hatching, chick rearing (February to March) causes increased energy demand since the chick must be provisioned regularly (Charrassin et al. 1998). It is likely that changes in foraging behaviour reflect how these predators access the most profitable oceanographic structures according to their time and energy constraints. In this context, the thermal structuring of the foraging area and the presence of different foraging niches may play an important role (Charrassin & Bost 2001).

South Georgia is situated within the Antarctic Circumpolar Current (ACC), the most pronounced feature of the Southern Ocean circulation (Rintoul et al. 2001). It includes 3 major deep-reaching fronts, from north to south, the SubAntarctic Front (SAF), the Polar Front (PF) and the southern ACC Front (SACCF) (Orsi et al. 1995). The PF is an important foraging area for incubating king penguins at South Georgia (Trathan et al. 2008, Scheffer et al. 2010). However, there is no information on how changing breeding constraints may affect foraging behaviour, and how this may relate to local oceanography. For king penguins, foraging areas close to the SACCF have not yet been considered, despite the key role of this front for the Scotia Sea ecosystem (Thorpe et al. 2002b, Thorpe et al. 2004, Ward et al. 2002, Murphy et al. 2004) and its close proximity to the breeding colonies at South Georgia. We know very little about features in the vertical dimension that may restrict efficient foraging for diving predators such as king penguins, or how this may relate to any changing constraints for these birds. Identifying such features and their association with different oceanographic areas may increase our understanding of how horizontal habitat use by diving predators is related to their exploration of the water column. This may be of importance in the context of environmental change, and any future

potential effects on king penguin populations (Le Bohec et al. 2008, Forcada & Trathan 2009, Péron et al. 2012).

We investigated how king penguins breeding at South Georgia explore their available foraging area over the summer season in the horizontal and vertical dimensions. Using a combination of Global Positioning System (GPS) tracking and time-depth-temperature recorders (TDR), we addressed the question of how horizontal habitat use may relate to different ACC frontal zones and associated thermal structuring of the water column, and how diving behaviour, presumably targeting particular niches in the water column, changed accordingly (see p.9 for the definition of “niche”). The results are discussed in the context of environmental variability and the potential vulnerability of diving predators such as king penguins to future environmental change.

3.3 Material and Methods

3.3.1 Study area, study period and device deployments

The study was conducted at the Hound Bay king penguin breeding colony on the northeast coast of South Georgia (54.23° S, 36.15° W) during the austral summers of 2005 to 2006 and 2006 to 2007. In total, 17 adult breeding king penguins were tagged: (1) during incubation in December 2005 to January 2006 (Early Incubation, $n = 4$, female), (2) during late incubation in January to February 2007 (Late Incubation, $n = 4$, unknown sex) and (3) during brooding ($n = 9$, unknown sex). Brooding birds were subsequently distinguished into Brooding I and Brooding II based on behaviour (see ‘Results’).

The horizontal movements of penguins were tracked by Track-Tag GPS loggers (Navsys; further details of Track-Tag are available at www.navsys.com/Products/tracktag.htm), which require only 60 ms to store raw GPS data. Devices were programmed to record

positions at 60 s intervals and were equipped with a saltwater switch to delay acquisition while birds were under water. Loggers, with batteries and housing, weighed 55 g (<0.5% of body mass) and measured $35 \times 100 \times 15$ mm (<0.7% of the cross sectional area of the body). Diving behaviour was recorded by TDR (Wild life Computers). TDR devices were programmed to record depth and water temperature at 1 s intervals when wet. Recordings during surface periods were halted by a saltwater switch and resumed when the bird restarted diving. The resolution of depth recordings was 0.5 m. TDRs weighed 30 g (<0.25% of body mass) and measured $15 \times 100 \times 15$ mm (Mk9) and $10 \times 90 \times 20$ mm (Mk7) (<0.5% of the cross sectional area of the body). Of the 17 penguins equipped with GPS devices, 13 of them had Mk9 TDR with external fast-responding temperature sensors, 2 had Mk7 TDR and 2 were without TDR devices. Devices were attached using methods modified from Wilson et al. 1997. All devices were recovered after a single foraging trip (varying between 5 and 23 d). In 2007, all tracked birds were weighed before leaving for sea and after their return to land to determine body mass gain during the foraging trips.

3.3.2 Oceanography of the study area

South Georgia is a sub-Antarctic island situated within the path of the ACC, with the PF to the north and the SACCF close to the island (Fig. 3.1). In contrast to most other king

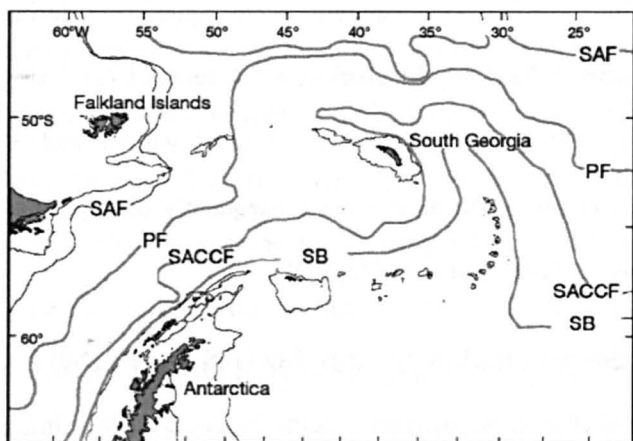


Figure 3.1: South Georgia and the Antarctic Circumpolar Current (ACC) frontal positions in the Scotia Sea. Fronts are shown by thick grey lines, the 500m and 1000m isobaths are marked in dark grey. Frontal positions are from Orsi et al. 1995 and Trathan et al. 1997; 2000. SAF: Sub-Antarctic Front; PF: Polar Front; SACCF: Southern ACC Front, SB: Southern ACC Boundary.

penguin breeding colonies which are located north of the PF (Bost et al. 2009), South Georgia is situated south of the PF. The PF is commonly defined as the location where cold Antarctic subsurface waters sink below warmer sub-Antarctic waters (Deacon 1933), corresponding to the northernmost extent of the subsurface temperature minimum, $< 2^{\circ}\text{C}$ near 200 m depth (Belkin & Gordon 1996).

The flow regime close to South Georgia is dominated by the SACCF, which loops anticyclonically around the South Georgia peri-insular shelf before retroflecting north of the island (Orsi et al. 1995, Thorpe et al. 2002b, Meredith et al. 2003a) at $\sim 36^{\circ}\text{W}$. The SACCF flow is rich in nutrients (Ward et al. 2002), and hosts high biomass of zooplankton (Murphy et al. 2004). The Antarctic Zone (AAZ) is situated between the PF and the SACCF; it is characterized by the meeting of cold Antarctic waters and warmer surface waters from the PF. A complex eddy field has been described in the AAZ north of South Georgia as well as a warm-core anticyclonic circulation at around 52°S , 35°W (Meredith et al. 2003a). Recent definitions of ACC fronts and zones in terms of Sea Surface Height (SSH) allow the identification of such features from altimetry data (Sokolov & Rintoul 2009, Venables et al. 2012), and the assignation of specific thermal profiles to frontal zones (Venables et al. 2012). In the Scotia Sea, the vertical structure of the water column includes the Surface Mixed Layer (SML), and the underlying cold Winter Waters (WW) originating from the previous winter mixed layer. The SML and WW are separated by a thermocline, a strong vertical temperature gradient of variable extent and intensity. Below the WW layer (from ~ 250 to 300 m), temperatures rise towards 2°C , characterizing the Circumpolar Deep Water (CDW).

3.3.3 Oceanographic data

SSH data

Changes in SSH encountered by the penguins over their foraging trips were analyzed using Aviso (www.aviso.oceanobs.com) absolute dynamic topography (ADT) data. We used Near-real time (NRT) data available at a higher temporal resolution than the delayed time (DT) products. Data were available at a spatial resolution of $1/3^\circ \times 1/3^\circ$ and a bi weekly temporal resolution. SSH values at each dive location were estimated by searching for the geographically nearest value within the corresponding dataset.

Vertical temperature data

Vertical temperature values were obtained from the external Mk9 sensor data after applying appropriate temperature correction factors from the device calibration data sheets (Wildlife Computers). Mk7 temperature data were not used due to long response times of the internal temperature sensors. Mk9 temperature sensors provide high quality data (accuracy $0.1^\circ\text{C} \pm 0.05^\circ\text{C}$; temperature sensor lag 1s, Simmons et al. 2009), and were, therefore, used for determining the properties of the water column encountered during the penguins' dives. To compensate for the surface heating effect by direct sun exposure and penguin body temperature on the temperature sensors (McCafferty et al. 2007), temperature values collected between 0 and 10 m were replaced by the value measured at 10 m depth during the ascent. The vertical water temperature gradient for each recorded depth point was also calculated; this was estimated as the temperature difference between 25 m above and 25 m below the given depth point. Temperature gradients near to the depth extremes of a dive were calculated using the maximal depth range possible (limited by the surface for points <25 m depth, and by the maximal dive depth for points $>\text{max. depth}$ 25 m). The resulting possible bias in gradient values may only affect the depth range between the maximum depth range of a dive and 25 m above, as dives < 50 m were not considered

for analyses of foraging behaviour (see Data analysis). A temperature gradient of 1 thus corresponds to a temperature increase of 1°C per 50 m depth, –1 to a temperature decrease of 1°C per 50 m.

3.3.4 Data analysis

Data analyses were performed using Matlab (MathWorks) and the custom-made software Multi- Trace (Jensen software systems).

Analysis of surface and diving behaviour

GPS data were filtered to remove positions with navigation class >2, where class categories were 0: good, 1: altitude aided, 2: marginal position dilution of precision, and 3: bad. For each bird, we calculated trip duration, distance covered, max. distance from the colony and the furthest latitude south reached. Exact departure and return times from and to the island were determined from the TDR data. A foraging zone coefficient (FZC) was calculated as the total trip length (km) divided by the max. distance from the colony (km) (modified from Guinet et al. 1997, Hull et al. 1997), indicating the degree of directness or looping of a foraging trip.

A zero offset correction was applied on the dive data. Only dives >50 m depth were used for analysis, as they were considered to represent the majority of king penguins foraging dives (Pütz et al. 1998, Charrassin et al. 2002). Diving behaviour was analysed by calculating the following dive parameters: dive depth, dive duration, bottom duration (the time between the first and last wiggle or dive step deeper than 75% of the maximum dive depth, following Halsey et al. 2007), the number of wiggles (deviations >1 m of depth with an absolute vertical instant > 0) as a proxy of feeding success (Bost et al. 2007) and broadness index (bottom duration:dive duration, indicating the proportion of a dive used for the bottom period, see Halsey et al. 2007 for more details). Furthermore, we determined

the total vertical distance travelled per day, the dive frequency, the percentage of submerged time compared to the total time at sea, and the percentage of submerged time spent at depths >150 m as proxies of foraging effort. As king penguins are visual feeders and essentially forage during the daylight and twilight hours (Bost et al. 2002), night dives were excluded from the analyses. Exact sunrise and sunset times were calculated as described in Scheffer et al. (2010). Geographical coordinates at the start of each dive were interpolated based on time from the GPS data, assuming straight line travel and constant speed between 2 location points (Weavers 1992).

Principal Component Analysis (PCA) was carried out on 15 variables characterizing foraging behaviour (surface movements and diving behaviour, see Table 3.1 for the complete listing of all PCA variables), allowing identification of the main variables accounting for differences in foraging behaviour as well as behavioural groupings of birds. Dive parameters among grouped birds were compared using Kruskal-Wallis statistics as tests for normality failed (Jarque Bera test) and transformations did not help the data to conform to the normality assumption. When significant differences were found among groups, an all pairwise multiple comparison (Dunn's method) was performed to determine the groups that differed from the others.

Analysis of horizontal and vertical habitat use

The horizontal habitat use of king penguins was analysed with respect to trip orientation relative to the different ACC fronts. The ACC fronts and zones were defined based on SSH signatures following Venables et al. (2012). The penguins' vertical habitat use was analysed with respect to the exploration of depth and thermal properties of the water column relative to the ACC fronts. We considered the bottom phases of dives, which is thought to be the most important phase for prey capture (Charrassin et al. 2002, Simeone & Wilson 2003, Ropert-Coudert et al. 2006). Kernel density estimations of bottom periods of

the different foraging groups were computed on SSH and depth using a Gaussian Kernel. These were then overlaid on the vertical thermal structure of different ACC frontal zones following Venables et al. (2012). This allowed us to analyse the penguins' use of the water column with respect to depth and thermal structures relative to frontal zones.

Detailed use of the water column by the penguins while foraging was analysed by considering depth, temperature and temperature gradient during the bottom periods of the dives. Analyses were carried out on data with a resolution of 1 Hz. Contour plots of bottom periods of dives >50 m on depth – temperature gradient and temperature – temperature gradient axes allowed us to evaluate the penguins' use of the water column, and to identify the target of different water masses by the different foraging groups. To identify water masses from the water characteristics targeted by the penguins, we defined 4 water masses based on water temperature (T) and temperature gradient (gradT): thermocline waters ($T \geq 1.5$; $\text{gradT} < 0$), WW in proximity ≤ 25 m of the thermocline ($T < 1.5$; $\text{gradT} < 0$), WW deeper than 25 m below the thermo cline ($T < 1.5$; $\text{gradT} \geq 0$), CDW ($T \geq 1.5$; $\text{gradT} \geq 0$).

Wiggles occurrence and influencing factors

As wiggles are good proxies of prey capture attempts in penguins (Takahashi et al. 2004, Bost et al. 2007, Hanuise et al. 2010), we examined water characteristics where wiggles occurred, with respect to temperature and temperature gradient. We used logistic regression models to quantify relationships between water properties and the occurrence of wiggles for individual as well as for grouped birds. For the regression models, we included temperature and temperature gradient data for dives >50 m depth with a temporal resolution of 1 s, after testing for non-correlation using Pearson's correlation coefficient. The predictor of wiggles occurrence was a combination of the water temperature, the values and the absolute values of the temperature gradient, taking into account the direction of the gradient as well as its intensity. To evaluate model discrimination

performances between wiggle presence and absence, we used risk score plots (Royston & Altman 2010). Risk score plots allowed us to graphically compare the densities of the risk score (linear predictor) in the event and no-event group (occurrence and non-occurrence of wiggles). The overlap of the risk score densities determined the discrimination performance of the model: the larger the overlap, the weaker the discrimination.

3.4 Results

3.4.1 Identification of different foraging groups

We distinguished 4 foraging groups characterized by differences in breeding stage as well as foraging characteristics (Fig. 3.2, Tables 3.1, 3.2 & 3.3). The groups were Early Incubation (n = 4), Late Incubation (n = 4), Brooding I (n = 3) and Brooding II (n = 4). The PCA of foraging parameters showed the separation of the 4 foraging groups, and allowed the identification of the main variables accounting for the differences (Fig. 3.2, Table 3.1). The first principal component was mainly explained by the horizontal and vertical

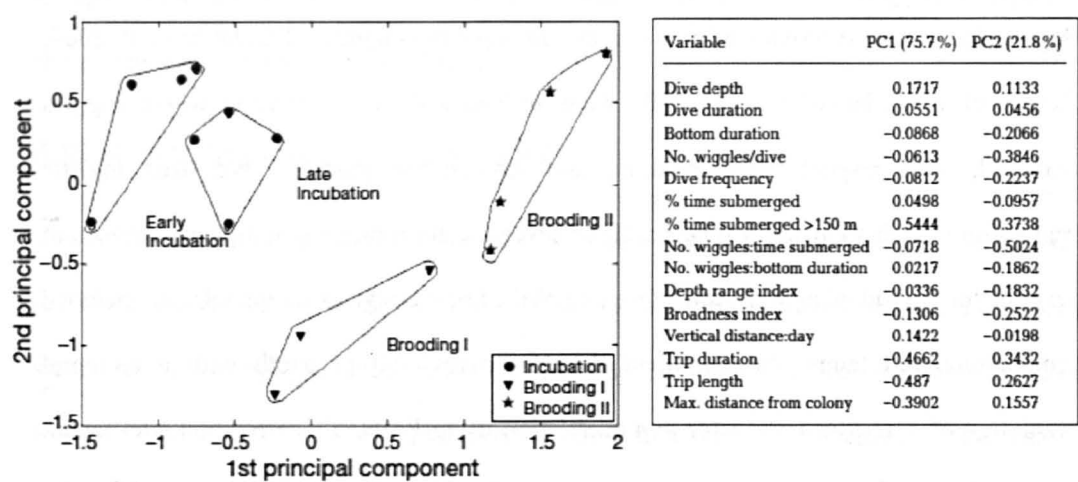


Figure 3.2: Principal component analysis of the foraging parameters in the different foraging groups. The component loadings of the variables are listed in Table 1.

Table 3.1: Principal component analysis of the foraging parameters: Component loadings of the different variables.

distances travelled. These variables separated the Brooding II from the Incubation groups, with the Brooding I birds spread out in between. Brooding II birds were characterized by the shortest horizontal (Table 3.2) and longest daily vertical (Table 3.3) distances travelled. The second principal component was mainly loaded with variables of underwater foraging behaviour, separating the Brooding I birds from the Incubation and Brooding II groups.

Brooding I birds were characterized by a dominant bottom phase, high wiggle numbers and a high dive frequency (Table 3.3). Brooding II birds showed the deepest and longest dives with the shortest bottom periods (Table 3.3). Broadness index was highest for Brooding I birds and lowest for Brooding II birds (Table 3.3). A main variable influencing both principal components was the proportion of dive time spent at depths >150 m, separating the Brooding II birds from the Incubation and Brooding I groups (Fig. 3.2, Table 3.1).

3.4.2 Trip orientation and foraging areas

All trips were oriented to the north towards the SACCF, AAZ and PF waters, with birds of different breeding stages targeting different foraging areas (Fig. 3.3) and showing different foraging trip characteristics (Table 3.2). Early Incubation birds undertook the most extended foraging trips, where increased SSH values indicated PF and Polar Frontal Zone (PFZ) waters. Late Incubation birds targeted areas at the southern edge of the PF and in the AAZ.

Brooding birds undertook shorter trips into areas south of the PF. Brooding I birds showed highly directed foraging trips into AAZ waters, indicated by low Foraging Zone Coefficient (FZC) values. Brooding II birds were characterized by less directed foraging trips into the SACCF or its northern boundary.

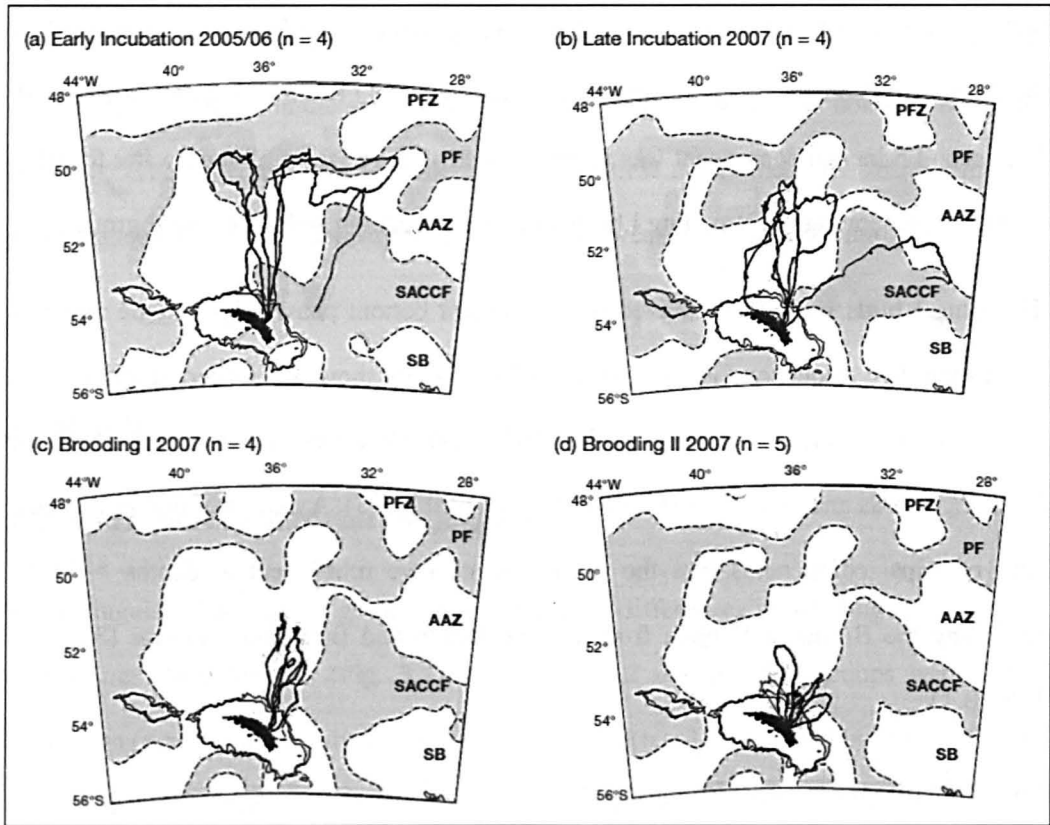


Figure 3.3: Tracks of GPS-equipped king penguins from South Georgia during summer 2005/06 and summer 2007 with the major ACC fronts in the Scotia Sea (a-d). Incomplete tracks are due to tag memory limitations and/or insufficient time at the surface to collect GPS satellite ephemerides. Frontal zones are based on Sea Surface Height (SSH) definitions from Venables et al. (2012). Frontal positions shown on the maps correspond to the mean positions over the trip period of the corresponding foraging group. PFZ: Polar Frontal Zone; PF: Polar Front; SACCF: Southern ACC Front; SB: Southern ACC Boundary.

Bird ID	Date of deployment and recovery	Trip duration (d)	Trip length (km)	Max. distance from colony (km)	Min. °S reached	FZC
Early Incubation						
8	23.12.2005–13.01.2006	19.9	2077	642	49.84	3.2
9	28.12.2005–18.01.2006	19.5	2291	522	49.77	4.4
10	30.12.2005–17.01.2006	16.4	1880	520	49.83	3.6
11	30.12.2005–23.01.2006	23.2	2510	537	49.73	4.7
Mean ± SE		19.7 ± 1.4	2190 ± 136	556 ± 29	49.79 ± 0.03	4.0 ± 0.3
Late Incubation						
C5	02.02.2007–20.02.2007	17.3	1585	435	50.77	3.7
C7	02.02.2007–2.02.2007	20.3	1506	409	50.72	3.7
C9	03.02.2007–26.02.2007	23.2	1690	558	51.82	3.0
C10	03.02.2007–17.02.2007	13.4	1150	445	50.40	2.6
Mean ± SE		18.6 ± 2.1	1483 ± 117	462 ± 33	50.93 ± 0.31	3.2 ± 0.3
Brooding I						
H5	09.02.2007–17.02.2007	6.1	610	234	52.55	2.6
H9 (no TDR)	12.02.2007–19.02.2007	6.2	559	227	52.5	2.5
P3	18.02.2007–01.03.2007	9.1	925	317	51.67	3.1
P5	18.02.2007–28.02.2007	7.0	822	346	51.32	2.9
Mean ± SE		7.1 ± 0.7	729 ± 87	281 ± 30	52.01 ± 0.31	2.8 ± 0.1
Brooding II						
H3	09.02.2007–16.02.2007	5.1	491	190	52.98	2.6
H6 (no TDR)	10.02.2007–16.02.2007	5.5	490	159	53.04	3.1
P4	18.02.2007–25.02.2007	6.0	517	163	53.50	3.2
P10	27.02.2007–04.03.2007	4.8	430	112	53.44	3.9
T4	28.02.2007–06.03.2007	5.5	629	247	52.20	2.4
Mean ± SE		5.4 ± 0.2	512 ± 33	174 ± 22	53.03 ± 0.23	3.0 ± 0.3

Table 3.2: Trip parameters for individual birds in the different foraging groups (FZC = Foraging Zone Coefficient).

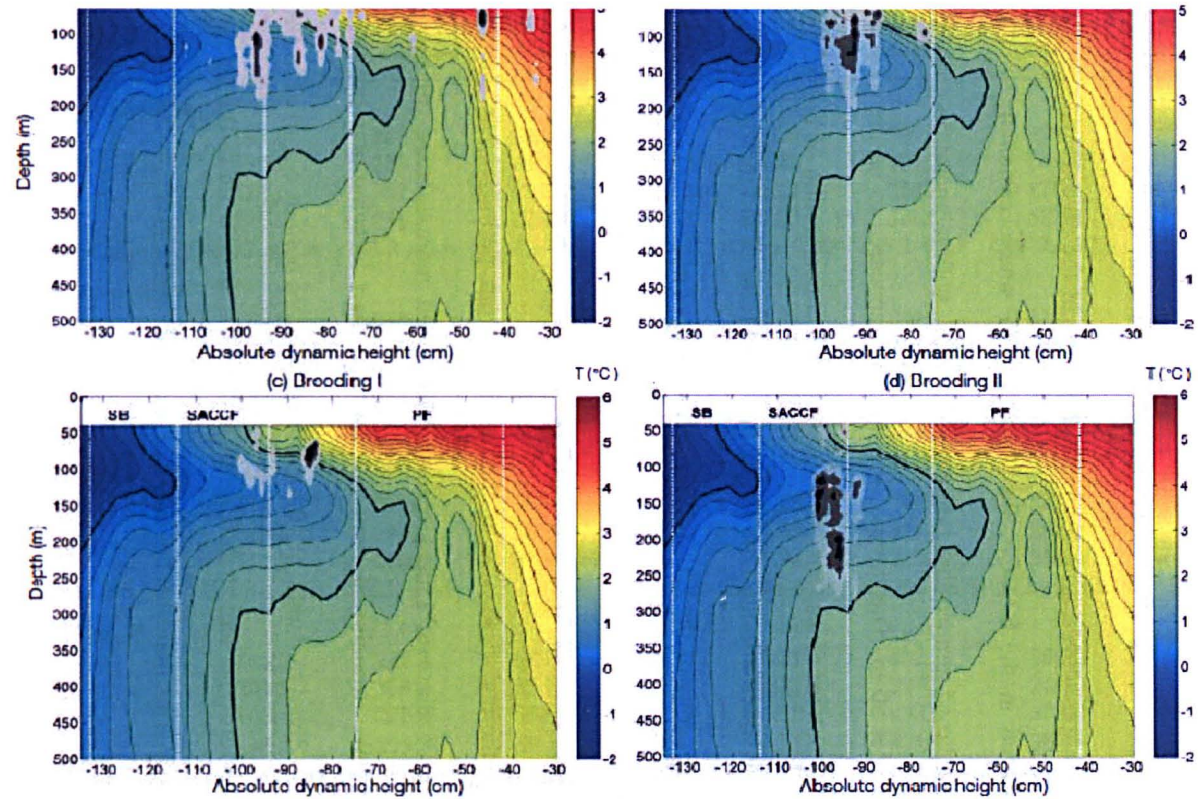
Table 3.3: Dive parameters for individual birds in the different foraging groups. KW = Kruskal Wallis test with $p < 0.001$. Dunn's test was performed with $p < 0.05$. The foraging groups show significant differences from others as indicated (all: all other foraging groups; Inc: Early and late incubation; BI: Brooding I; BII: Brooding II).

Bird ID	Dive depth (m)	Dive duration (s)	Bottom duration (s)	Wiggles per dive	Broadness index	Total VD (km d^{-1})	Total dives per day	% of time submerged >150 m
Early Incubation								
8	117.8	246.5	61.6	6.3	0.26	305.5	268.5	2.3
9	130.2	259.0	73.1	8.0	0.28	305.2	209.4	4.7
10	129.0	287.4	92.2	9.1	0.32	265.1	171.0	3.5
11	126.0	260.5	82.6	12.4	0.32	301.8	583.0	3.4
Mean \pm SE	125.7 \pm 2.8	263.3 \pm 8.6	77.4 \pm 6.6	9.0 \pm 1.3	0.30 \pm 0.02	295.1 \pm 9.7	308.0 \pm 93.8	3.5 \pm 0.5
Late Incubation								
C5	134.2	246.8	61.9	10.5	0.25	310.1	412.5	4.1
C7	128.8	260.9	73.3	7.4	0.28	315.1	249.7	4.1
C9	144.1	258.6	54.1	7.1	0.21	297.7	261.3	4.6
C10	122.5	251.4	57.8	5.7	0.23	364.2	361.5	3.1
Mean \pm SE	132.4 \pm 4.6	254.4 \pm 3.3	61.8 \pm 4.1	7.7 \pm 1.0	0.24 \pm 0.02	321.8 \pm 14.6	321.2 \pm 39.4	4.0 \pm 0.3
Brooding I								
H5	145.1	256.0	70.9	9.7	0.28	434.8	327.3	6.4
P3	118.0	249.8	96.2	14.6	0.39	317.1	254.2	2.0
P5	111.3	239.0	81.0	10.4	0.34	333.6	355.4	2.1
Mean \pm SE	124.8 \pm 10.3	248.3 \pm 4.7	82.7 \pm 7.4	11.6 \pm 1.5	0.33 \pm 0.03	361.8 \pm 36.8	312.3 \pm 30.2	3.5 \pm 1.4
Brooding II								
H3	163.8	272.2	57.9	8.8	0.21	432.2	294.2	8.4
P4	201.9	308.4	52.1	6.5	0.17	377.5	249.0	10.8
P10	183.4	288.8	55.5	5.3	0.19	437.6	199.0	12.7
T4	175.8	294.2	68.1	11.4	0.24	424.9	366.4	9.6
Mean \pm SE	181.2 \pm 8.0	290.9 \pm 7.5	58.4 \pm 3.4	8.0 \pm 1.3	0.20 \pm 0.01	418.0 \pm 13.8	277.2 \pm 35.5	10.4 \pm 0.9
KW & Dunn's test	all	BI-BII	BI-BII	BI	BI-BII	Inc-BI&BII	BII	BII

3.4.3 Vertical habitat use

Penguins in the different foraging groups showed differing use of the water column in the various ACC zones (Fig. 3.4), targeting different depths, water temperatures and temperature gradients during the bottom periods of the dives (Fig. 3.5). Early Incubation birds foraged in the SACCF, the AAZ, the PF and occasionally in PFZ waters, and explored a broad temperature range of -1 to 6°C , with temperature gradients between 0.5 and -3°C per 50 m. The thermocline and WW appeared to be the most important water masses for bottom times, but there was no clear concentration of bottom times in specific parts of the water column. Late Incubation birds foraged in the SACCF and in the AAZ to the southern edge of the PF. Bottom periods were directed into waters of -0.5 to 2°C and temperature gradients of up to -4°C per 50 m. Shallow and deep WW were the most targeted water masses. Brooding I birds showed highly focused targeting of shallow waters of strong thermal gradients in the AAZ. Bottom periods were directed into similar conditions to those of Late Incubating birds, but more focused on strong gradients in shallow WW. Brooding II birds concentrated their foraging activity in SACCF waters, where they dived to depths of 100 to 300 m. Bottom periods occurred in a restricted range of temperature and temperature gradient of -0.5 to 2°C and -0.5 to 0.5°C per 50 m, respectively. This indicates the target of deep WW and CDW.

Figure 3.4: Kernel densities of bottom times for the different foraging groups (a-d). Density contours encompass 20, 50 and 90% of the bottom time distributions. Temperature profiles on Sea Surface Height (SSH) and depth with ACC front limitations from Venables et al. (2012).



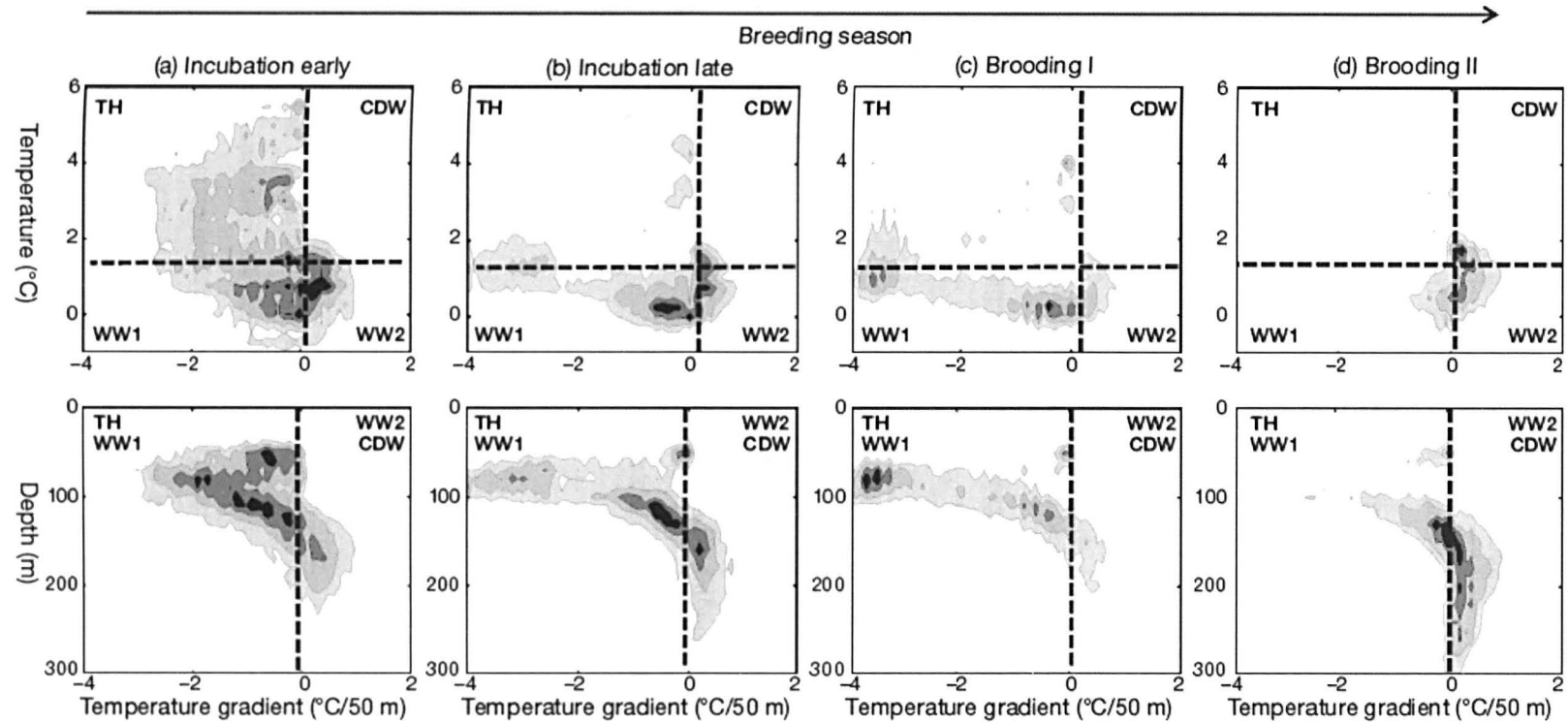


Figure 3.5: Environmental niches in the water column targeted by the different foraging groups (a-d). Plotted are bottom times of all dives deeper than 50 m on temperature, temperature gradient and depth axes. Contours encompass 10, 25, 50 and 90% of the bottom times of each foraging group. Black dotted lines indicate the limits of the water column characteristics used for the definition of the water masses (see Material and Methods). TH = Thermocline; WW1 = shallow Winter Water close to the thermocline; WW2 = deeper Winter Water; CDW = Circumpolar Deep Water.

3.4.4 Wiggles occurrence and influencing factors

For incubating birds, the correlations between wiggle occurrence and water properties were generally weak when considered over an entire foraging trip. In the PFZ, low water temperature appeared to play a more important role for wiggles occurrence than the temperature gradient (Fig. 3.6 a,b). The logistic regression model showed that wiggle occurrence was greater at negative water temperature gradients for Brooding I birds, and increasing with positive gradient for Brooding II birds (Fig 3.6c,d). Correlations were stronger for Brooding I than for Brooding II birds. Risk score plots indicated better model discrimination performances for conditions of wiggles absence than of wiggles presence for all birds, and reduced performances for grouped birds compared to the analysis of single birds.

3.4.5 Body mass gain of tracked penguins

Brooding II birds had highest body mass gains per day as well as in relation to horizontal and vertical distances travelled. Brooding I birds showed higher mass gains per day and distances travelled than the Incubation group (Table 3.4).

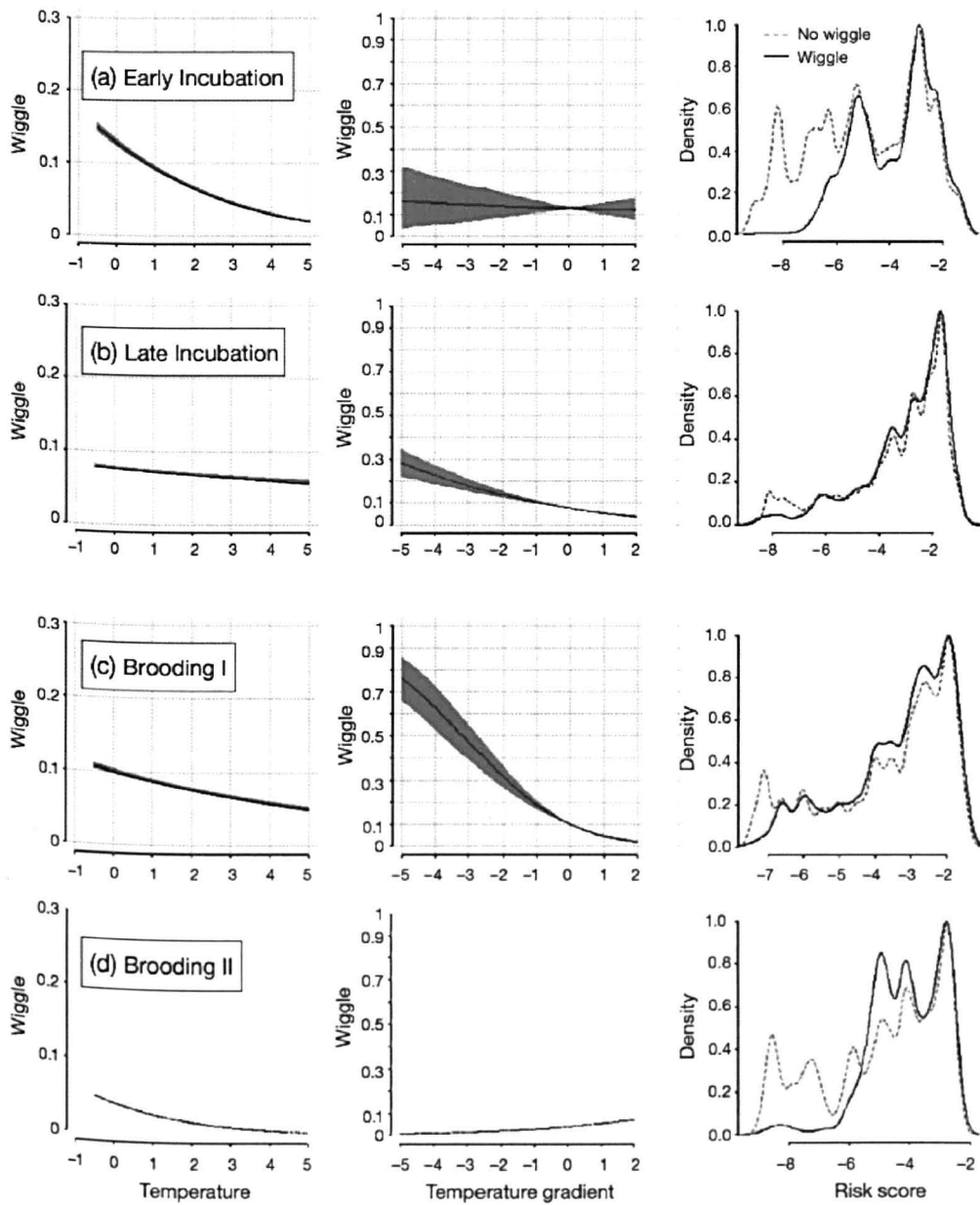


Figure 3.6: Wiggles occurrence as a function of water temperature and temperature gradient, and corresponding risk score plots for model discrimination performance. Output of the logistic regression model and risk score plots for a – one Early Incubation and b – one Late Incubation bird. Early Incubation includes data from only within PF and PFZ waters, Late Incubation includes data from the entire trip. c,d – Model output and risk score plot for (c) one Brooding I and (d) one Brooding II bird.

Table 3.4: Body mass at start and end of foraging trips as well as total body mass gain per day and per distance travelled for king penguins tracked in 2007. HD = horizontal distance; VD = vertical distance.

Bird ID	Start weight (kg)	End weight (kg)	Mass gain		
			(kg d ⁻¹)	(kg per 100 km HD)	(kg per 100 km VD)
Late Incubation					
C5	11.4	15.4	0.23	0.25	0.07
C7	11.4	17.0	0.28	0.34	0.09
C9	11.0	14.2	0.14	0.19	0.05
C10	11.8	14.6	0.21	0.24	0.06
Mean ± SE	11.4 ± 0.2	15.3 ± 0.6	0.21 ± 0.03	0.26 ± 0.04	0.07 ± 0.01
Brooding I					
H5	13.8	15.8	0.33	0.33	0.08
H9	13.8	16.9	0.50	0.55	no TDR
P3	12.1	15.1	0.33	0.32	0.10
P5	14.1	17.0	0.42	0.35	0.12
Mean ± SE	13.5 ± 0.5	16.2 ± 0.4	0.39 ± 0.04	0.39 ± 0.06	0.10 ± 0.01
Brooding II					
H3	14.0	16.8	0.55	0.57	0.13
H6	13.0	15.8	0.51	0.57	no TDR
P4	13.8	15.9	0.35	0.41	0.09
P10	12.0	14.5	0.46	0.58	0.10
T4	15.1	17.9	0.58	0.44	0.14
Mean ± SE	13.6 ± 0.5	16.0	0.49 ± 0.04	0.51 ± 0.04	0.12 ± 0.01

3.5 Discussion

This is the first study to investigate how a deep diving avian marine predator changes its foraging behaviour and habitat use at a fine spatial scale, both vertically and horizontally. The major features of our study are: (1) King penguin foraging behaviour showed different horizontal and vertical patterns over the summer season, presumably in response to changing energetic constraints related to their breeding phase. Foraging trips during incubation extended to the PF, whereas brooding birds foraged exclusively south of the PF in AAZ and SACCF waters. (2) Diving behaviour was correlated with the thermal structure of the water column, with the vertical temperature gradient and depth appearing to play important roles for the separation of different vertical foraging habitats. (3) Structure in the hydrological environment south of the PF may allow foraging strategy adjustment in relation to changing constraints, and may offer important flexibility for king penguins in the context of environmental variability.

3.5.1 Foraging areas in relation to frontal zones

Areas used for foraging by king penguins changed over the course of the summer season. Birds explored the PF during early incubation and the waters between the PF and the SACCF later in the summer season. For seabirds, changes in foraging trip duration at different times of the breeding cycle are known to occur and are thought to be the result of changing time constraints arising from the need to supply the chick with food (Bost et al. 1997, Charrassin et al. 1999, Lescroel & Bost 2005). However, in contrast with the situation at South Georgia, king penguins breeding at other locations have not been reported as changing their foraging areas between incubation and brooding (Bost et al. 1997, Guinet et al. 1997, Sokolov et al. 2006). The accessible region to the north of South Georgia is influenced by 2 major ACC fronts, both representing potential areas of increased mesoscale variability (Trathan et al. 1997, Trathan et al. 2000, Moore et al.

1999b, Thorpe et al. 2002b, Meredith et al. 2003b), and, therefore, the possibility of alternative foraging locations for marine predators. The role of the PF has already been reported for king penguins breeding at South Georgia (Trathan et al. 2008, Scheffer et al. 2010) and at other locations (Bost et al. 1997, 2009, Moore et al. 1999a, Charrassin & Bost 2001, Sokolov et al. 2006). At South Georgia, the AAZ and SACCF appear to provide alternative foraging areas closer to the colony. It may allow short foraging trips with low travel costs for birds with high time and energy constraints, as shown by brooding birds, and may, therefore, play a key role for king penguins. It may also be that seasonal changes in oceanography may lead to more favourable circulation patterns and/or increased productivity at the SACCF, making it a preferable foraging area for king penguins during brooding.

The importance of the SACCF for the Scotia Sea ecosystem has been emphasised in previous studies (Thorpe et al. 2002b, Thorpe et al. 2004, Ward et al. 2002, Murphy et al. 2004) due to nutrient enrichment resulting in increased phyto- and zooplankton development, possibly resulting in increased myctophid densities associated with these more productive waters. In the AAZ, the meeting of Antarctic waters with warmer PFZ waters as well as the presence of SACCF eddies (Thorpe et al. 2002b, Meredith et al. 2003a) may create areas of strong thermal gradients, where myctophids may aggregate (Brandt et al. 1981, Kozlov et al. 1991). Reduced vertical mixing in the AAZ compared to adjacent frontal areas may increase the stability of such thermal structures, therefore favouring associated prey patches (Spear et al. 2001).

King penguins have already been reported to use mesoscale oceanographic features for non-random directed foraging during incubation at South Georgia (Trathan et al. 2008, Scheffer et al. 2010) and at Crozet islands (Cotté et al. 2007). Seasonal changes between foraging areas associated with different larger-scale oceanographic features of elevated

mesoscale activity support the hypothesis that king penguin alter their foraging behaviour at different spatial and temporal scales.

3.5.2 Targeted foraging habitats in the water column

Our detailed analysis of the time spent at the bottom of the dives, relative to frontal zones and to thermal structures in the water column, allowed us to determine the water masses explored by king penguins over the summer season, and how birds adjust their foraging niches according to breeding constraints.

During December and January, incubating birds foraged in the SACCF, the AAZ and the PF, and targeted various thermal structures at different depths in the water column. Enhanced vertical mixing in frontal areas (Spear et al. 2001) may lead to increased spatial and temporal variability in thermal structures and associated prey resources. Such dynamic prey distributions may be reflected by the less consistent targeting of specific depth-temperature- gradient patterns of birds foraging in the PF compared to in the AAZ, and only weak correlation of wiggle occurrence with specific temperature gradients.

Late Incubation and Brooding I birds mainly foraged in AAZ waters. Brooding I birds targeted shallow WW in close proximity to the thermocline, and the occurrence of wiggles was correlated with strong thermal gradients. The importance of sub-thermocline prey aggregations has already been reported for dolphins (Scott & Chivers 2009), tuna (Schaefer et al. 2007) and sunfish (Cartamil & Lowe 2004), and appears to be confirmed for king penguins foraging in the AAZ. Collins et al. (2008, 2012) found that certain myctophid species can be present at shallow depths during daytime in the AAZ in the area to the north of South Georgia. Strong thermal gradients of high stability may represent suitable conditions for stable myctophid aggregations at shallow depths, which have been

reported previously associated with warm-core rings in the Gulf Stream (Conte et al. 1986) and in the equatorial Atlantic Ocean, with tuna also exploiting these aggregations (Marchal & Lebourges 1996, Bard et al. 2002). The diving behaviour of Brooding I birds may indicate the presence of such permanent myctophid layers at shallow depths of 70 to 110 m in the Scotia Sea, even though this has so far only been reported from more temperate regions. However, this hypothesis remains speculative as independent prey data was not available for our study.

Brooding II birds showed significantly deeper dives than the other groups, mainly targeting waters with weak positive temperature gradients at the transition between deep WW and CDW in the SACCF. High body mass gains despite increased dive depths and reduced bottom times suggest increased foraging efficiency in these deep waters. Deep and long dives reported from king penguins at Crozet in autumn (Charrassin et al. 1998, 2002, Halsey et al. 2010) suggest seasonal changes in targeted prey similar to those observed at South Georgia for Brooding II birds. At Crozet, king penguins appear to compensate increased costs for deeper dives in autumn by longer bottom times (Charrassin et al. 2002, Halsey et al. 2010). At South Georgia, king penguins seem to be able to increase foraging efficiency at the bottom of dives. The foraging area targeted by Brooding II birds may provide particular conditions of highly profitable prey resources at great depths, potentially enhanced by the higher nutrient content in areas with the SACCF influx into the Scotia Sea (Ward et al. 2002).

3.5.3 Thermal structure of the water column and foraging

The thermal structure of the water column and depth appeared to play a crucial role for the separation of foraging niches and the expression of different foraging patterns, especially with increasing constraints on the animals. Relative water structures have been suggested to play an important role for vertical movements of other marine predators such as tuna

and billfish (Brill et al. 1993, Brill & Lutcavage 2001, Brill & Lutcavage 2001), sunfish (Cartamil & Lowe 2004), dolphins (Scott & Chivers 2009) and basking sharks (Sims et al. 2005). Foraging tuna and associated tropical seabirds have been reported to be more abundant in non-frontal areas characterized by lower vertical mixing and higher stability of vertical thermal structures (Owen 1981, Spear et al. 2001). King penguins are diving predators that target similar prey; they may, therefore, rely on the same criteria for favourable foraging habitats and show similar affinity with well structured waters, possibly reflected by targeting distinct niches in non-frontal or border areas by brooding birds. In addition to the importance of frontal zones for Southern Ocean marine predators (Bost et al. 2009), non-frontal or boundary areas with a higher stability of vertical thermal structures may also play a key role for diving predators such as king penguins, especially when constraints limit flexible travel times and behavioural adaptations to dynamic conditions at fronts.

The vertical temperature gradient appeared to be a main factor for foraging niche adjustment and explaining differences in prey pursuit behaviour (wiggle occurrence). Thermal gradients are locations of enhanced biological activity (Thomas & Emery 1988, Lima et al. 2002), resulting in the accumulation of biomass for various trophic levels, ranging from planktonic organisms to mesopelagic fish and ultimately upper trophic level predators. Being one of the most pronounced vertical temperature gradients in the ocean, the thermocline has already been suggested as an important feature for king penguins at Crozet (Charrassin & Bost 2001) as well as for other marine predators foraging in the Southern Ocean (Boyd & Arnborn 1991, Biuw et al. 2007) and in more temperate regions (Cayre & Marsac 1993, Kitagawa et al. 2000, Spear et al. 2001, Weng et al. 2009, Sepulveda et al. 2010). Our study underlines the crucial role of the thermocline for foraging king penguins breeding at South Georgia. It also demonstrates the possibility that

king penguins have alternate efficient foraging strategies for exploiting water masses where thermal gradients do not seem to be the main factor governing prey distribution.

Our regression models have revealed some insights into the effect of thermal properties of the water column on king penguins foraging. However, variable regression coefficients between individual birds as well as the prevalence of Brooding I and Brooding II patterns on identical trip departure dates underline the fact that foraging strategies might not only relate to particular environmental conditions. Behavioural plasticity and individual factors (Svanback & Bolnick 2005, Sargeant et al. 2007) such as detailed breeding constraints, fitness and prior experience may also play a role. Lower model performances for wiggles presence than absence may result from the fact that favourable foraging conditions for king penguins are not only determined by the thermal structure of the water column, but may also be influenced by other factors governing prey distribution in a given environment such as stochastic processes and prey behaviour, or the presence of predators.

3.5.4 King penguins' foraging and environmental variability

Foraging behaviour of king penguins breeding at South Georgia appears to be structured both horizontally and vertically. Penguins targeted different foraging areas depending on their breeding constraints, and adjusted their foraging activity in the water column. So far such strong habitat selection and the presence of alternative foraging niches have not been reported for king penguins from other locations. Patterns described from Crozet suggest changes in foraging characteristics over the summer season similar to those described at South Georgia, with shortening of foraging trips and increasing dive depths. However, penguins in both the incubation and brooding stage target the PF, and foraging patterns appear less diverse than those of king penguins at South Georgia with respect to trip characteristics, diving behaviour and the targeting of distinct niches in the water column (Charrassin et al. 1998, 2002, Charrassin & Bost 2001). This may suggest that alternative

foraging areas closer to the colony, as reported from South Georgia, are not available at Crozet.

For king penguins breeding north of the PF (i.e. Crozet, Marion Island), the geographically nearest profitable myctophid aggregations may be found at accessible depths mostly at the PF and its northern edges, as myctophid species targeted by king penguins are known to increase in depth northwards of the PF (S. Fielding pers. comm.). This means that penguins breeding in these locations may depend to a higher degree on the PF. Predicted declines of king penguins due to environmental variability (Barbraud et al. 2008, Le Bohec et al. 2008, Péron et al. 2012) and shifts in the PF may, therefore, only relate to areas where the animals are highly dependent on the PF due to the lack of alternative foraging areas. Such predictions might be of lesser value for king penguins breeding at South Georgia.

King penguins at South Georgia appear to be able to exploit profitable prey resources at the southern edge and south of the PF, either in terms of reduced depth in the AAZ or of increased profitability per catch effort at the bottom in SACCF waters. The area south of the PF may offer an elevated degree of foraging habitat segmentation to king penguins, as other structures than the PF may provide for profitable prey resources at accessible depths. King penguins from Heard Island, also located south of the PF, appear mainly to forage in the area to the east of the island (Moore et al. 1999a, Wienecke & Robertson 2006), a location influenced by the southern branch of the PF and the Fawn Trough current (Roquet et al. 2009, van Wijk et al. 2010). Foraging in areas outside or at the southern boundaries of the PF, areas characterized by cold water masses, may produce similar patterns to those at South Georgia. However, studies from Heard Island provide no information on diving behaviour in relation to the thermal structure of the water column, or on segregation of foraging areas.

Oceanography at South Georgia is known to be influenced by ENSO (El Niño – Southern Oscillation) and SAM (Southern Annular Mode) as well as more direct atmospheric processes (Trathan & Murphy 2002, Meredith et al. 2008). However, different time lags between these events and the response in oceanography at South Georgia occur (Meredith et al. 2008), as well as temporal variation in the connections within the Scotia Sea ecosystem (Murphy et al. 2007). Our study includes reports of only one season per foraging group. Therefore, it remains open as to whether the patterns observed are a constant element in the foraging strategy of king penguins breeding at South Georgia, or whether they are a response to particular conditions during our study years. Nevertheless, the oceanographic patterns observed during our study appear to be consistent with general patterns described in the area to the north of South Georgia (Trathan et al. 1997, Trathan et al. 2000, Thorpe et al. 2002b, Meredith et al. 2003b, Brandon et al. 2004). Also, the temporal and spatial scales of the oceanographic features considered exceed the duration of the tracked foraging trips. Low sample sizes of the different foraging groups may raise questions about conclusions on general behavioural patterns at a population level. Even so, the foraging patterns observed during brooding indicate the presence of optional foraging niches close to shore at South Georgia, allowing foraging of potentially increased efficiency, at least in some years. This might also play a key role in potential responses of king penguins to environmental changes (Forcada & Trathan 2009), as optional foraging niches may allow them to better adjust foraging behaviour in response to the prevailing oceanographic conditions.

Chapter 4

Foraging behaviour of king penguins

breeding at Kerguelen in relation to oceanography



4.1 Abstract

Investigating the responses of marine predators to oceanographic features in their foraging area is of key importance for understanding the animals' foraging behaviour and their reproductive success. In this study we examined the foraging behaviour of king penguins breeding at Kerguelen (south Indian Ocean) in relation to oceanographic features in their foraging area. We used ARGOS and Global Positioning System (GPS) tracking together with Time-Depth-Temperature-Recorders (TDR) to follow the at-sea movements of king penguins. Combining the observed penguin behaviour with oceanographic data at the surface through satellite data and at depth through in-situ recordings by the penguins enabled us to explore how such predators adjust their horizontal and vertical movements in response to their physical environment.

King penguins foraged in the area to the south-east of Kerguelen during incubation and brooding, which is dominated by an influx of cold waters of southern origin which interacts with Antarctic Polar Frontal (PF) waters. Incubating penguins extended foraging trips into offshore areas where they explored the PFZ, PF and AAZ. During brooding, the penguins foraged in areas closer to the colony with mainly PF signatures. Penguins of both breeding stages explored the cold-water influx in proximity of the Kerguelen Plateau shelf break, with foraging trips of incubating birds extending further south along the cold-water influx. Foraging at depth took mainly place in the Surface Mixed Layer (SML), the thermocline and Winter Water (WW), with patterns of WW exploration coinciding with the cold-water influx from the south. In southern areas, the penguins also explored Circumpolar Deep Water (CDW), which appeared to be related to the cold-water influx. Penguins of both breeding stages showed highest foraging performances in the SML and thermocline. Overall, the meso-scale interaction of the cold-water influx with the PF appears to be of key importance for foraging king penguins breeding at Kerguelen.

4.2 Introduction

The foraging behaviour of marine predators is dependent upon the horizontal and vertical distribution of their prey (Hunt et al. 1999). Prey distribution is, in turn, influenced by the physical properties of the water column, including such factors as temperature and temperature gradient (Owen 1981; Franks 1992); factors which also help characterize different water masses within the ocean. Thus, the horizontal and vertical patterns of water mass distribution also govern prey distribution in terms of species composition and prey patch properties, including patch density and size (Collins et al. 2008, 2012). Oceanographic structure and water mass distribution therefore play a crucial role for marine predators influencing their horizontal and vertical movements when seeking prey.

The Southern Ocean hosts major biomasses of top predators such as whales, seals and penguins. King penguins are important avian predators of the Southern Ocean (Woehler 1995; Bost et al. 2012). They rely mainly on myctophids (Myctophidae: lantern fish) (Cherel & Ridoux 1992), mesopelagic fish that are generally associated with particular water masses or temperature ranges (Hulley 1981; Kozlov et al. 1991) as well as with fronts and related oceanographic features (Brandt et al. 1981; Pakhomov et al. 1996; Rodhouse et al. 1996). The horizontal and vertical distribution of water masses is therefore of key importance for foraging predators such as king penguins. King penguins are known to explore their foraging habitat in a non-random way, targeting large- and mesoscale surface features such as fronts and eddies (Cotte et al. 2007; Trathan et al. 2008; Scheffer et al. 2010) as well as specific water masses and thermal features within the water column (Charrassin & Bost 2001; Scheffer et al. 2012) during prey search. However, we still have little knowledge about how these oceanographic features might be used as cues and so lead to efficient foraging, or about how an animal might be adapted to its local oceanographic conditions close to its breeding location.

The Kerguelen archipelago is situated on the extensive Kerguelen Plateau in the south Indian Ocean. The Kerguelen Plateau is a major bathymetric obstruction in the eastward flow of the Antarctic Circumpolar Current (ACC), significantly steering and channelling most of the deep-reaching ACC flow (Park et al. 2008b; Sokolov & Rintoul 2009; Park & Vivier 2011). The juxtaposition of flows of different origins and properties, local bathymetrically-related upwellings and channellings of flows (Park et al. 2009; Roquet 2010) together with iron enrichment from the island and peri-insular shelf (Blain et al. 2001; Blain et al. 2007) create highly dynamic and productive areas downstream of the Kerguelen Plateau. The steering effects of the Kerguelen Plateau bathymetry may furthermore lead to increased spatial stability for some oceanographic processes, creating oceanographic features of high predictability in close proximity to various species breeding colonies (Cherel & Weimerskirch 1995; Guinet et al. 2001). Due to the high levels of productivity in the waters surrounding the island and given its relative isolation within the Southern Ocean, the Kerguelen Plateau hosts very high abundances of marine predators, including penguins, petrels and seals (Weimerskirch et al. 1989; Hindell et al. 2011).

The most prominent oceanographic features in the area to the south-east of Kerguelen are the Polar Front (PF) and the Fawn Trough Current (FTC), both of which are part of the ACC. The PF has been identified to flow eastwards across the northern Kerguelen Plateau just south of Kerguelen (Park et al. 1998; Charrassin et al. 2004; Park et al. 2008b, Park & Vivier 2011), then wraps anticyclonically around the island from the south-east to continue its flow north-eastward, and then flows again south-eastwards along the east of the Kerguelen Plateau (Park & Vivier 2011). The FTC is a strong current flowing along the southern edge of the Northern Kerguelen Plateau through the Fawn Trough, a deep passage (<2800 m) separating the Southern and the Northern Kerguelen Plateau and channelling an important part of the ACC flow (Park et al. 2008b; Roquet et al. 2009). At depth, the FTC is characterized by the northern limit of Winter Water (WW), corresponding to the

subsurface temperature minimum (T_{\min}) of 0°C situated at around 100 m depth (Roquet et al. 2010), and the southern limit of Upper Circumpolar Deep Water (UCDW), corresponding to the mid-depth temperature maximum (T_{\max}) of 2°C (Roquet et al. 2010; van Wijk et al. 2010; Park & Vivier 2011). Most of the FTC is deflected south-eastwards by the Chun Spur, a pronounced bathymetric feature at the south-eastern end of the Northern Kerguelen Plateau. However, a part of the shallower waters (corresponding to the cold WW layer, ~100m depth) is advected northwards across the Chun Spur to the south-east of Kerguelen (Park et al. 2008b; Roquet et al. 2010). The cold WW advected from the Fawn Trough over the Chun Spur flows northwards along the eastern shelf break of the Kerguelen Plateau, forming a cold-water subsurface tongue that can extend up to the latitude of Kerguelen (Charrassin et al. 2004; Park et al. 2008b; van Wijk et al. 2010), where it reaches depths of ~100 m (Charrassin et al. 2004). Because of its unique characteristics of cold waters of Antarctic Zone origin, these waters originating from the FTC can be clearly distinguished from the warmer surrounding waters (Roquet et al. 2010).

King penguins are important avian predators breeding at Kerguelen (Bost et al. 2012), comprising an estimated 342 000 breeding pairs, quickly increasing (Chamaillé-Jammes et al. 2000; Bost et al. 2012, last estimate dating to 1999). During the summer season, king penguins generally explore the area to the south-east of Kerguelen during their brooding and crèche foraging trips (Koudil et al. 2000; Charrassin et al. 2002; Bost et al. 2002; Pütz et al. 2002; Charrassin et al. 2004; Bost et al. 2011; Hindell et al. 2011). Studies on brooding birds have shown that birds forage in areas close to the shelf break, where they explore the subsurface tongue of cold water originating from the FTC (Charrassin et al. 2002; Charrassin et al. 2004). However, there is currently no knowledge about the detailed foraging patterns of birds of different breeding stages, or the oceanographic features they explore in either the horizontal or vertical dimensions.

In this study we investigated the foraging behaviour of king penguins breeding at Kerguelen in relation to oceanographic features within their foraging area. Using Argos and GPS together with TDR tracking data, we studied the penguins' detailed surface and diving behaviour during incubation and brooding. Combining the behavioural data with remote-sensing (Sea Surface Temperature, Sea Surface Height) and in-situ (water temperature from the TDR sensors) data, we investigated how the bird's behaviour may relate to oceanographic features in the horizontal and vertical dimension such as frontal zones and different water masses at depth.

4.3 Material and Methods

4.3.1 Study area, study period and device deployments

Our study took place at the Ratmanoff king penguin breeding colony on the east coast of Kerguelen Island (70.55°S, 49.24°E). The Ratmanoff colony is one of the most important breeding colonies at Kerguelen, comprising 52 000 of the estimated 342 000 breeding pairs at Kerguelen (Bost et al. 2012). Fieldwork was conducted during the austral summers of 1998 and 1999 and those between 2006 and 2011, generally between January and March and on incubating and brooding birds. In total 84 adult king penguins were tagged, 31 during incubation and 53 during brood.

The horizontal movements of king penguins were tracked using two types of device: (1) Argos Platform Terminal Transmitters (PTT); and (2) Fastloc GPS loggers (Sirtrack, NZL) configured to record positions at 60 second intervals and equipped with a saltwater switch to delay acquisition while birds were under water. This later type was used since the season 2009/10.

Diving behaviour was recorded with time-depth recorders (Mk9 devices; Wildlife Computers, Redmond, USA) with fast-responding external temperature sensors, allowing to investigate the penguins' diving behaviour in relation to their hydrological environment at depth. The TDR devices were programmed to record depth and water temperature at 1 s intervals; they weighed 30 g in air (<0.25% of body mass) and measured 15 × 100 × 15 mm (<0.5% of the cross sectional area of the body). Information on the sizes, weights and years of use of the tracking devices are shown in Table 4.1.1.

DEVICE	Dimensions (cm)	Section (cm ²)	Weight (g)	Years of use
PTT: Telonics St10	18.0 ^a x 2.5 ^b	4.9	270	1998-2002
PTT: Sirtrack Kiwisat 101	13.8 ^a x 14 ^c x 2.9 ^d	4.1	208	2002-2012
TDR: MK9	6.7 ^a x 1.7 ^c x 1.7 ^d	2.9	30	2002, continuing
GPS: Sirtrack Fast Loc 1G-138A	9.2 ^a x 5 ^c x 2 ^d	10	127	2010, continuing

Table 4.1: Overview of sizes, weight and years of use of Argos PTT, GPS and TDR devices in the tracking of king penguins at Kerguelen used for this study. a: length; b= diameter; c: width; d: height . All the dimensions are indicated in cm.

In total 38 birds were equipped with Argos and 7 with GPS devices only, 16 with TDR devices only, and 26 with both TDR and Argos/GPS. A summary of the number of tracked birds and device types deployed in the different years is given in Table 4.1.2.

Devices were attached using methods modified from Wilson et al. 1997. All devices were recovered after a single foraging trip (varying between 5 - 51 days, some trip durations were unknown during 2010). Tracked birds were weighed before leaving for sea and after their return to land to determine body mass gain (BMG) during the foraging trip.

Year	Incubation	Brooding
1998	--	15 Argos only
1999	4 Argos only	8 Argos only
2006	3 Argos + Mk9	6 Argos + Mk9 1 Argos only
2007	2 Argos + Mk9	5 Argos + Mk9
2008	2 Argos + Mk9 1 Argos only 1 Mk9 only	1 Argos + Mk9
2009	--	4 Argos + Mk9 9 Mk9 only
2010	9 Argos only 2 Mk9 only	--
2011	3 GPS + Mk9 4 Mk9 only	4 GPS only
Total birds equipped	31	53

Table 4.2: Overview of study birds equipped with GPS, Argos and/or TDR devices with successful data retrieval.

4.3.2 Environmental data

Bathymetry and slope data

Throughout our habitat analyses, we used the **Smith and Sandwell Global Seafloor Topography from Satellite Altimetry and Ship Depth Soundings (NOAA and Scripps Institution of Oceanography)** (Smith & Sandwell 1997) at a spatial resolution of 2' x 2'.

More details are available at http://gcmd.nasa.gov/records/GCMD_SIO_NOAA_SEAFLOORTOPO.html. Bathymetric slope was calculated as the maximum slope value within a 5×5 moving window of grid cells across the bathymetry grid.

Remotely sensed oceanographic data

Sea surface height (SSH) data: We used absolute dynamic topography (ADT) Delayed time (DT) data from Aviso (www.aviso.oceanobs.com). Data were available at a spatial resolution of 1/3° x 1/3° and a weekly temporal resolution. ACC fronts and zones were defined based on SSH signatures following Venables et al. (2012). These frontal signatures were defined based on the Scotia Sea, but are stated to be valid for other locations of the Southern Ocean (Venables et al. 2012).

Vertical temperature data and definition of different water masses

Vertical temperature values were obtained from the external TDR Mk9 sensor data. TDR Mk9 temperature sensors provide high quality data (accuracy 0.1° C±0.05°C, Simmons et al. 2009), and were therefore used for determining the properties of the water column encountered during a penguins' dives. For each dive, temperature data that were recorded during the descent and ascent phases were projected onto a vertical axis corresponding to the maximum depth of the dive and averaged at a 1-m depth interval. This resulted in regularly gridded temperature data in the vertical plane, and facilitated calculation of the

average potential differences in the water column properties encountered during the descent and ascent phases due to horizontal movements of the penguins. A 5 m moving average filter was then applied to the temperature profiles, allowing for correction of any potential measurement errors from the TDR temperature sensors without smoothing out thermal discontinuities in the water column. To compensate for the surface heating effect by direct sun exposure and penguin body temperature on the temperature sensors (McCafferty et al. 2007), temperature values collected between 0 and 10 m were replaced by the value measured at 10 m depth during the ascent. Based on the regularly gridded temperature profiles we calculated the vertical water temperature gradient for each depth point; this was estimated as the temperature difference between 25 m above and 25 m below the given depth point. Temperature gradients near to the depth extremes of a dive were calculated using the maximal depth range possible (limited by the surface for points <25 m depth, and by the maximal dive depth for points >maximum depth-25 m). The resulting possible bias in gradient values may only impact the depth range between the maximum depth range of a dive and 25 m above, as dives shallower than 50 m were not considered for analyses of foraging behaviour (see 4.3.3 Data analysis). A temperature gradient of +1 thus corresponds to a temperature increase of 1°C per 50 m depth, -1 to a temperature decrease of 1°C per 50 m. To identify water masses from the water characteristics targeted by the penguins we defined five water masses based on water temperature (T), temperature gradient (gradT) and depth (D): Surface Mixed Layer (SML) waters ($T \geq 2$; $-0.5 < \text{gradT} < 0$; $D \leq 100\text{m}$); Thermocline (TH) waters ($T \geq 2$; $\text{gradT} \leq -0.5$); Winter water (WW) ($0.5 < T < 2$; $\text{gradT} \leq 0$); cold WW ($T \leq 0.5$; $\text{gradT} \leq 0$); and Circumpolar Deep Water (CDW) and modified CDW (mCDW) ($\text{gradT} > 0$; $D > 100\text{m}$). For simplicity CDW and mCDW are named “CDW” unless stated otherwise. Based on these definitions a specific water mass was assigned to each depth grid point of each dive.

The resulting dataset thus consisted of temperature, temperature gradient and water mass profiles on a regular 1m depth grid for each dive.

4.3.3 Data analysis

Data analyses were performed using Matlab (The MathWorks, Inc., MA 01760-2098, USA) and the custom-made software MultiTrace (Jensen software systems, Laboe, Germany).

4.3.3.1 Analysis of surface behaviour

GPS data were downloaded from each device and decoded into GPS locations using manufacturer-supplied software (Sirtrack Fastloc software, version 1.5.0.2). Following the manufacturer's instructions, we excluded locations from the analysis when residual error values were greater than 30 or fewer than 6 satellites were used for location calculation (Sirtrack 2010). Argos data were processed with state-space models (Jonsen et al. 2003, 2005) in order to estimate the most probable locations taking into account measurement errors. The process model of the state space model uses transition equations based on correlated random walk models to estimate the most probable locations of an animals' path. As the observation model of the state-space model did not lead to a clear distinction of behavioural modes into travel and foraging, we used First-Passage Time (FPT) analysis in order to detect area-restricted search (ARS) behaviour from the GPS and the estimated Argos locations. FPT provides a measure of the time an animal takes to cross a virtual circle of a radius r that is moved along its track, assuming that high FPT in certain areas corresponds to ARS behaviour displayed by the animals (Fauchald & Tveraa 2003). For each location we assigned SSH, bathymetry and slope values by searching for the geographically nearest value within the corresponding dataset.

Kernel densities of foraging locations of incubating and brooding penguins were computed on latitude and longitude using a Gaussian Kernel (Matlab kde2d function, Botev et al. 2010). Locations at distances <30 km from the colony were excluded from the kernel density estimation to reduce the colony bias on the spatial distribution of the penguins. The kernel densities were then overlaid on the main oceanographic features in the foraging area (from Park et al. 2008b) to visualize potential associations of foraging with oceanography. Foraging habitat use in relation to oceanographic and bathymetric features was assessed using kernel densities of foraging locations on SSH and bathymetry.

For each bird, we calculated trip duration, distance covered, maximum distance from the colony and the furthest latitude south and east reached. Exact departure and return times from and to the island were determined from the TDR data for birds with Argos/GPS and TDR devices, and from field observations and visual inspection of surface tracks arriving at the colony for Argos/GPS data only.

4.3.3.2 Analysis of diving behaviour

A zero offset correction was applied on the dive data. Only dives deeper than 50 m depth were used for analysis, as they were considered to represent the majority of king penguins foraging dives (Pütz et al. 1998; Charrassin et al. 2002).

a - Calculation of dive parameters

Diving behaviour was analysed by calculating the following dive parameters: dive depth, dive duration, duration and start depth of the bottom phase (the time between the first and last wiggle or dive step deeper than 75% of the maximum dive depth, following Halsey et al. 2007), the number of wiggles (deviations >1 m of depth with an absolute vertical instant greater than 0) as a reliable proxy of feeding success (Bost et al. 2007; Hanuise et al. 2010). Furthermore, we determined the dive efficiency (DE), calculated as bottom duration

/ (dive duration + post-dive interval) following Ydenberg & Clark 1989. We also determined the product of dive rate \times bottom start depth as an indicator for the physiological effort due to diving activity, where dive rate was calculated as the number of dives $>50\text{m}$ carried out in an ± 30 minutes interval around each dive. From the TDR temperature sensor data, we determined the temperature at the start of each bottom phase, indicating the temperature where prey pursuit started.

b - Vertical profiles of diving behaviour and in-situ thermal properties of the water column

In addition to the dive parameters, each dive was furthermore characterized by the vertical thermal profiles of temperature, temperature gradient and water masses based on the Mk9 temperature sensor data (see sections 3.3.3 and 3.3.4). Corresponding to this vertical grid of water masses properties, we determined the accumulated bottom time and wiggle profiles spent in different water column properties and water masses for each dive, calculated as the summed bottom times and number of wiggles spent at each 1m-depth interval during the dive. This allowed analysis of proxies of foraging success (the total bottom times and wiggle numbers) spent in relation to the thermal structure of the water column.

The relative bottom times spent in different water masses were calculated as the proportion of the total bottom time of a dive spent in a particular water mass, ranging from 0 (no bottom time of a dive spent in the given water mass) to 1 (all the bottom time of a dive spent in the given water mass). This allowed the evaluation of the importance of the different water masses for prey pursuit during a given dive.

c - Interpolation of horizontal environmental parameters (oceanographic and bathymetric) for each dive

Exact sunrise and sunset times were calculated as described in Scheffer et al. (2010) based on nautical definitions of sunrise and sunset (twilight hours defined as the sun being geometrically 12° below the horizon) (US Naval Observatory Astronomical Applications Department). Geographical coordinates of the start of each dive were interpolated based on time from the GPS and the estimated Argos location data, assuming straight line travel and constant speed between 2 location points (Weavers 1992). For each dive location we assigned SST, SSH, bathymetry and slope values by searching for the geographically nearest value within the corresponding dataset. Dive locations were then assigned to frontal classes (PFZ, PF, AAZ, SACCF) based on SSH signatures following Venables et al. (2012), and to bathymetry classes based on depth and slope. Bathymetry classes were defined as shelf (depth ≤ 1000 , slope < 0.2), shelf break (depth $> 1000\text{m}$, slope ≥ 0.2) and offshore (depth > 1000 , slope < 0.2).

The resulting dataset of vertically gridded behavioural and oceanographic data at a fine scale together with the corresponding oceanographic surface and bathymetric properties for each dive allowed for a detailed analysis to be undertaken of changes in diving behaviour with environmental conditions in the horizontal and vertical dimension. It furthermore allowed for examination of whether birds select areas with particular water column properties, based on the dive locations.

As king penguins are visual feeders and essentially forage during the daylight and twilight hours (Bost et al. 2002), night dives were excluded from these analyses (corresponding to 16.7% of the total dives < 50 m depth, and 2.1% of the total dives > 50 m depth. However, for birds equipped with TDR devices only, geographical coordinates of the dives could not be calculated. For the approximate identification of sunrise and sunset, and the consequent

discharge of night dives from the analysis, we used the sunrise time at the easternmost and sunset time at the westernmost point reached by the foraging trips. This method allowed to exclude night dives from the analysis while being conservative for twilight hours, leading to including some night dives into the analysis instead of possibly discharging twilight dives if sunrise and sunset times were set too late or early, respectively.

Comparisons of dive parameters among breeding stages, frontal and bathymetry zones as well as among different water masses explored were carried out using Kruskal-Wallis tests as tests for normality failed (Jarque Bera test) and transformations did not help the data to conform to the normality assumption. When significant differences were found among groups, an all pairwise multiple comparison (Dunn's method) was performed to determine the groups that differed from the others.

d - Detailed analysis of foraging phases at depth in relation to frontal zones, bathymetry and water masses

Detailed use of the water column by the penguins while foraging was analysed by considering the bottom phase and wiggle numbers of the dives, as the bottom phase is thought to be the most important phase for prey capture (Charrassin et al. 2002, Simeone & Wilson 2003; Ropert-Coudert et al. 2006), and wiggles have been shown to be reliable indicators of prey capture by king penguins (Simeone & Wilson 2003; Takahashi et al. 2004; Bost et al. 2007; Hanuise et al. 2010). Bottom periods were analysed by considering temperature, temperature gradient and the water masses encountered. We evaluated the penguins' water masses use during bottom times using the following analyses and plots:

1 - Contour plots for the bottom periods for dives >50 m (plotted on temperature and temperature gradient axes) allowed us to evaluate the penguins' use of the water column,

and to identify whether they target different water column properties during incubation and brood.

2 - Changes in water mass exploration during bottom times in relation to ACC fronts and bathymetry were analysed considering SSH, depth and slope for incubating and brooding birds.

3 - Maps of relative bottom times spent in specific water masses on bathymetry and frontal zones allowed visualization of spatial changes in water column exploration during different breeding stages in relation to bathymetry and surface oceanographic features. The relative bottom times spent in WW and CDW were projected onto a latitude-longitude grid based on the dive locations. Horizontal interpolation of the relative bottom times between the dive locations was carried out using linear interpolation.

4 - The foraging performance of king penguins *in* the different water masses was assessed based on the cumulative number of wiggles and the dive efficiency (cumulative bottom time spent in a given water mass relative to the total dive time and post-dive surface interval), indicating the importance of the different water masses for prey pursuit.

4.3.3.3 Analysis of oceanographic data: Spatial patterns of the water column structure in the foraging area

From the in-situ TDR temperature data we assessed the fine-scale structure of the horizontal and vertical habitat in the foraging area explored by king penguins. From the vertical water mass profiles we determined the start depth of the different water masses in the water column, and projected this onto a latitude-longitude grid based on the dive locations. Horizontal interpolation of specific water masses start depths (of WW and CDW) between the dive locations was carried out using linear interpolation. The resulting

maps allowed visualization of spatial changes in the structure of the water column in the areas explored by king penguins as well as relations of such oceanographic structure at depth with bathymetry and surface oceanographic features determined from SSH.

4.4 Results

4.4.1 Foraging trip orientation in relation to bathymetry and oceanography

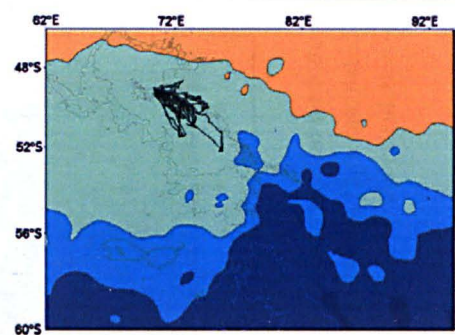
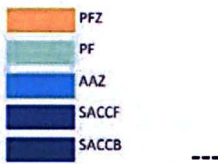
All foraging trips made by king penguins were oriented to the south-east or south of Kerguelen, with birds of different breeding stages showing different foraging trip characteristics (Table 4.3) and targeting areas of differing bathymetric and oceanographic properties (Fig. 4.1). Incubating birds undertook extended foraging trips to the south and east, reaching PFZ, PF and AAZ waters in offshore areas of depths up to 6000 m (Fig. 4.1, 4.2). Foraging locations for incubating birds coincided with areas at the shelf break or in offshore waters influenced by the cold-water subsurface current along the south-eastern shelf break of the Kerguelen Plateau, and with the area over the northern Chun Spur (Fig. 4.3a). Brooding birds undertook shorter foraging trips exclusively into PF waters, mostly concentrating on northern PF waters mainly at depths < 1000 m on the Kerguelen Plateau (Fig. 4.2). Foraging areas for brooding birds were mostly located over the shelf and at the shelf break to the south-east of the island, and only the outermost foraging locations reached areas impacted by the cold-water subsurface current used by incubating birds (Fig. 4.3b).

Foraging trip parameters showed higher levels of interannual variability for incubating birds than for brooding birds (Table 4.3). In particular the year 2010 was characterized by extreme values for incubating birds, with longer foraging trips extending further to the south-east than during any other year. A more detailed description of the environmental conditions and foraging behaviour during 2010 is reported in Chapter 5 below.

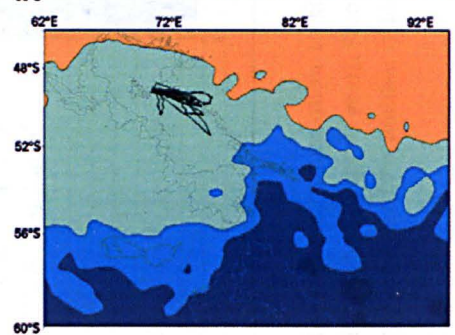
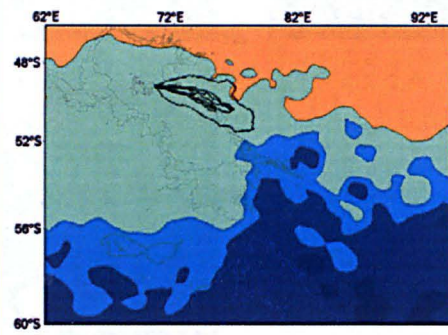
Incubation

Brooding

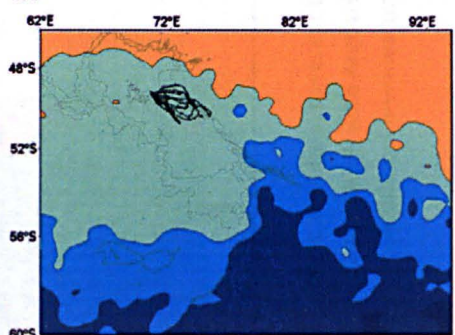
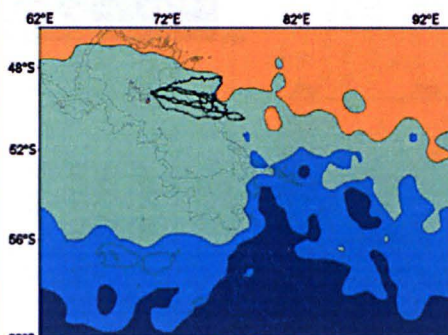
1998



1999



2006



2007

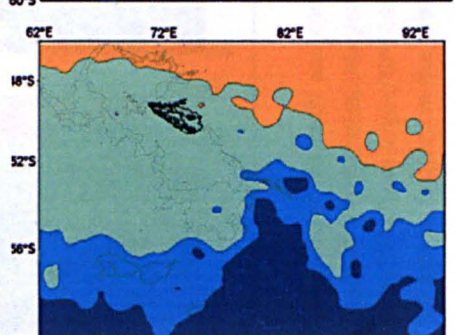
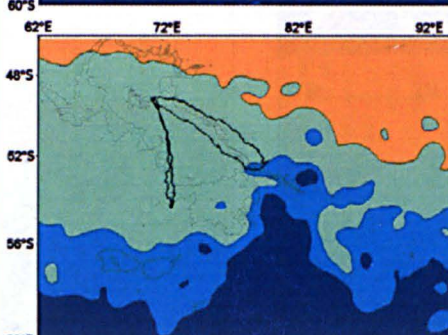


Figure 4.1: Trip orientation of Argos- and GPS-tracked birds in relation to bathymetry (grey contours: 0, 1000, 2000m depth) and frontal positions (coloured contours). Frontal zones are based on SSH signatures following Venables et al. (2012). Frontal positions on the maps correspond to the mean positions over the trip period of the corresponding foraging group during each year. PFZ: Polar Frontal Zone; PF: Polar Front; AAZ: Antarctic Zone; SACCF: Southern ACC Front; SACCB: Southern ACC Boundary.

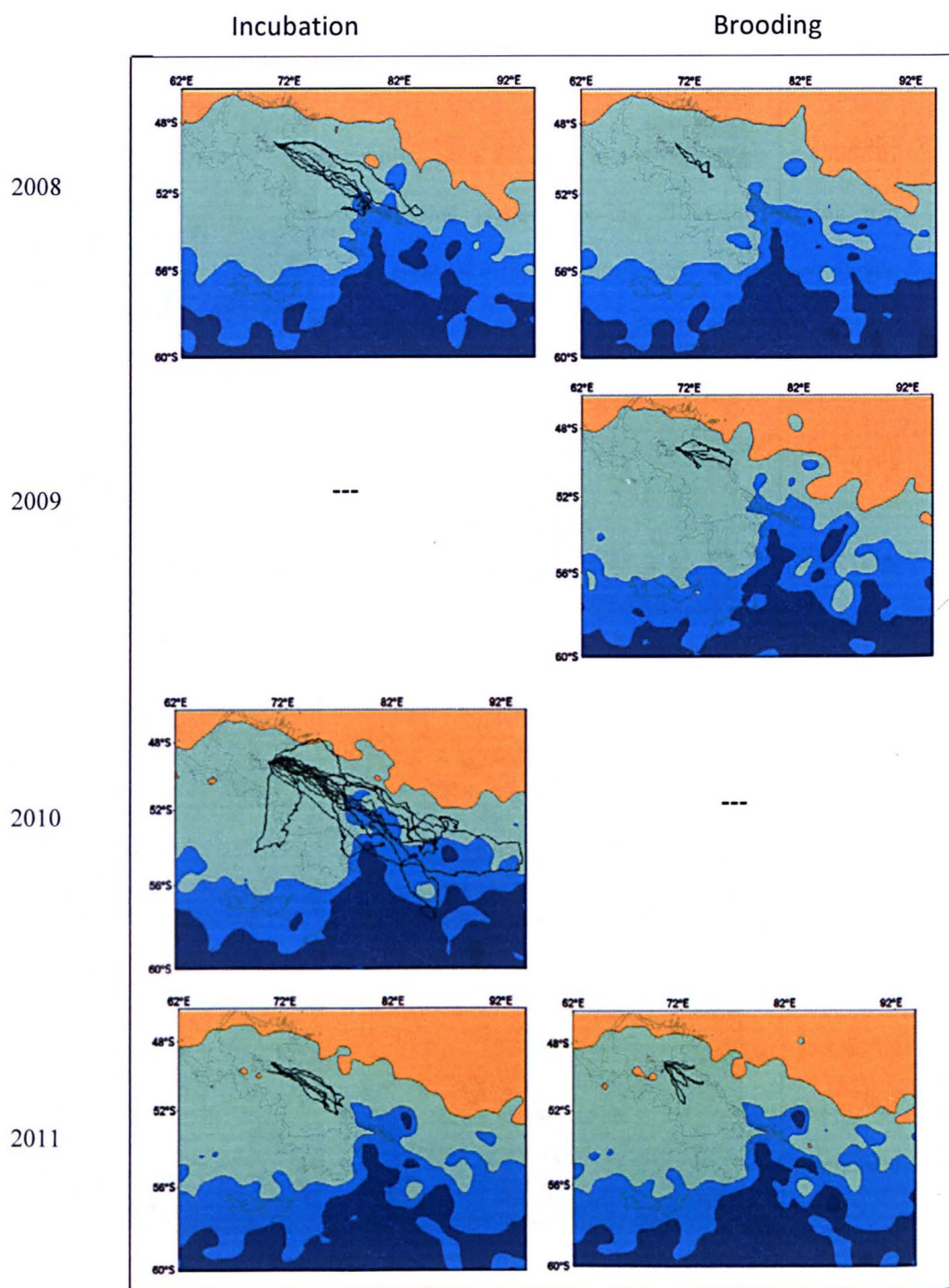


Figure 4.1 (continued).

Incubation												
year	month	n	trip duration (days) *	trip length (km)	max.dist. from colony (km)	max °S	max(max °S)	max °E	max(max °E)	BM trip start (kg) *	Body mass gain (kg) *	Body mass gain/day *
1998		0										
1999	Jan	4 (0; 4)	18.95 ±1.48	1242.5 ±118.03	481.13 ±47.73	50.76 ±0.26	51.54	76.76 ±0.61	78.34	9.85±0.36 (n=4)	3.1 (n=1)	0.17 (n=1)
2006	Jan	3 (3; 0)	21.19 ±1.89	1433.17 ±26.73	459.64 ±47.98	50.49 ±0.12	50.67	76.58 ±0.64	77.77	9.53±0.44 (n=3)	no data	no data
2007	Feb	2 (2; 0)	18.99 ±2.74	1645.66 ±163.82	634.85 ±78.07	53.55 ±0.88	54.43	75.87 ±3.58	79.44	9.85±0.45 (n=2)	2.25 ±1.35	0.11 ±0.06
2008	Feb	3 (2; 1)	31.39±1.01	2311.76 ±141.27	813.68 ±106.69	53.12 ±0.12	53.24	80.75±1.59	83.92	9.43±0.23 (n=3)	2.8 ±0.26	0.09±0.01
2009		0										
2010	Feb	9 (0; 9)	39.02 ±2.56 (n=11)	3021.17 ±389.64	991.98 ±152.67	54.01 ±0.73	57.69	82.76±2.28	93.7	9.88±0.15 (n=17)	3.96 ±0.21 (n=9)	0.11±0.01 (n=9)
2011	Feb	3 (0; 3)	23.86 ±1.28 (n=7)	1476.4 ±161.67	515.48 ±24.41	51.94 ±0.14	52.22	76.59 ±0.41	77.24	9.35±0.34 (n=7)	4.24±0.28 (n=7)	0.18±0.01 (n=7)
Mean±SE		24 (7; 17)	27.69±2.01	2091.08±2.08	717.24±72.60	52.56±0.4	57.7	79.24±1.04	93.7	9.65±0.33	3.16±0.21	0.12±0.01
Brooding												
year	month	n	trip duration (days) *	trip length (km)	max.dist. from colony (km)	max °S	max(max °S)	max °E	max(max °E)	BM trip start (kg) *	Body mass gain (kg) *	Body mass gain/day *
1998	Feb	15	8.58 ±0.52 (n=25)	710.12 ±68.72	244.55±24.74	50.55 ±0.21	52.23	73.18 ±0.29	75.83	11.36±0.19 (n=25)	1.86±0.17 (n=25)	0.23 ±0.03 (n=25)
1999	Feb	8	8.90 ±1.6	738.69 ±81.5	280.82 ±33.14	50.3 ±0.22	51.6	73.9 ±0.46	75.2	11.78±0.35 (n=5)	2.03±0.35 (n=4)	0.3±0.09 (n=4)
2006	Feb	7	8.57 ±0.87	682.98±81.08	244.24±31.60	50.28±0.15	50.76	73.47±0.45	75.21	11.43±0.22 (n=7)	2.3±0.22	0.3±0.04
2007	Feb	5	9.59 ±0.54	967.26 ±77.53	299.56 ±14.25	50.23±0.24	50.67	74.23 ±0.19	74.81	9.64±0.3 (n=5)	2.65 ±0.26	0.28 ±0.04
2008	Feb	1	11.2	901.41	308.82	51.07	51.07	73.92	73.92	10.75±0.35 (n=2)	2.3	0.21
2009	Feb	4	11.36 ±1.33 (n=11)	717.23 ±113.55	289.96±45.28	50.01 ±0.21	50.44	74.2 ±0.67	75.72	10.58±0.25 (n=11)	2.62 ±0.12 (n=11)	0.25 ±0.03 (n=11)
2010		0										
2011	Feb	4	9.23 ±0.72	674.27±39.48	249.37 ±19.49	50.54 ±0.41	51.57	73.14±0.37	74.12	11.03±0.42	1.73 ±0.27	0.19 ±0.04
Mean±SE		44	9.34±0.51	741.95±34.66	263.38±12.33	50.39±0.1	52.23	73.58±0.17	75.83	10.94±0.3	2.07±0.12	0.24±0.02
Control (Incubation only)												
year	month	n	trip duration (days)							BM trip start	BMG	BMG/day
2010	Feb	30	32.61±0.53							9.97±0.15	4.94±0.21	0.15±0.01
2011	Feb	25	17.87±0.82							9.80±0.19	3.38±0.19	0.19±0.01

Table 4.3: Trip and body mass parameters for study and control birds. N-Values represent the following information: total number of tracked birds during this year (number of birds with Argos/GPS + TDR during this year; number of birds with Argos/GPS only during this year). Parameters with * are calculated based on all tracked birds; without * include data from Argos/GPS birds only. Additional n-values are given where the number of birds used for the calculation was different from the number of tracked birds given in the table.

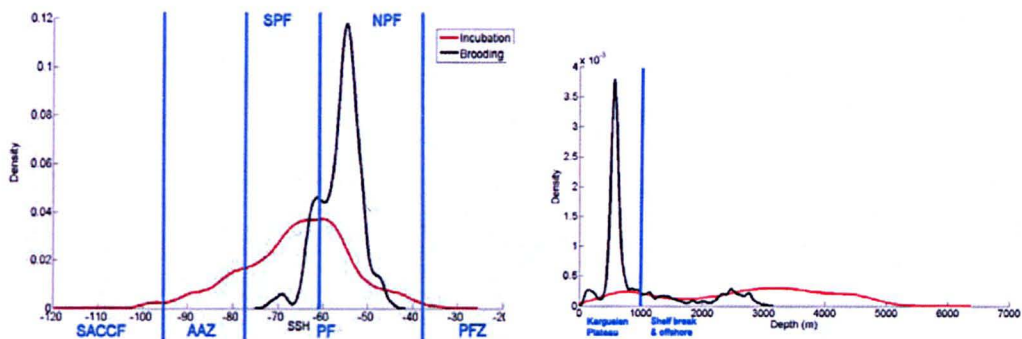


Figure 4.2: Density distributions of foraging locations of incubating (red) and brooding (black) birds in relation to SSH and bathymetry. PFZ: Polar Frontal Zone; PF: Polar Front; NPF: northern PF; SPF: southern PF; AAZ: Antarctic Zone; SACCf: Southern ACC Front. Frontal definitions are based on Venables et al. (2012).

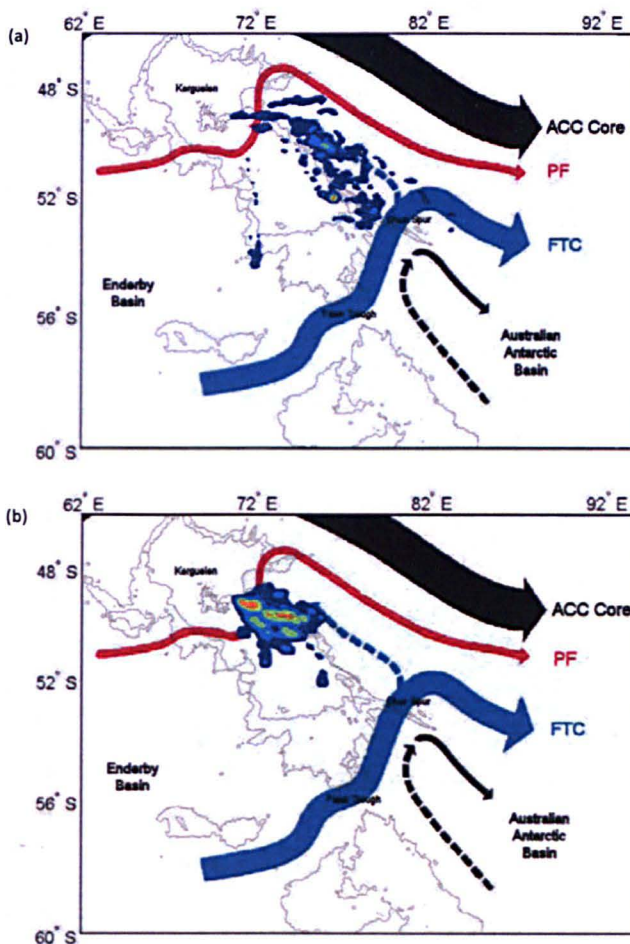


Figure 4.3: Kernel densities of foraging locations of the different breeding stages in relation to main oceanographic features and bathymetry in the foraging area. a- Incubation; b-Brooding.

Contours encompass 5, 25, 50 and 75 % of the foraging location distributions. Grey lines show bathymetry contours at 0, 1000 and 2000 m depth. Arrows show main oceanographic features in the foraging area following Park et al. (2008).

4.4.2 Body mass gain (BMG)

Incubating birds had higher levels of total body mass gain (BMG), whereas brooding birds showed higher mass gains per day (Table 4.3). Daily BMG decreased with foraging trip duration for both incubating and brooding birds (Incubation: $R^2=0.31$, Brooding: $R^2=0.3$) (Fig. 4.4). Brooding birds showed higher BMG for short foraging trips, but with a steep decrease with increasing trip duration. Daily BMG for incubating birds increased with the proportion of foraging locations in the PF ($R^2=0.27$) (Fig. 4.5). For brooding birds there was no apparent relation between BMG and the proportion of a foraging trip spent in different bathymetry zones (figure not shown).

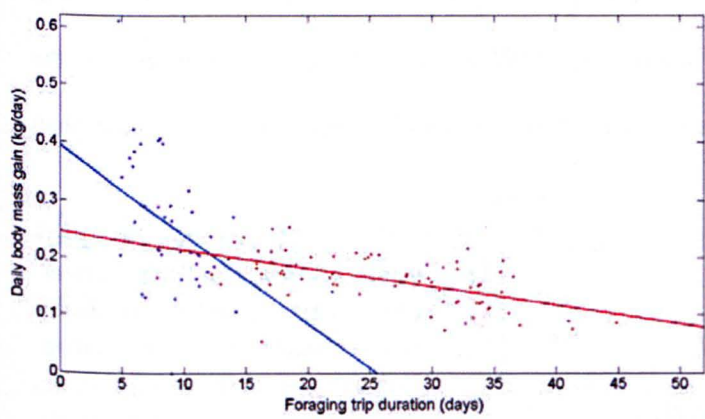


Figure 4.4: Daily body mass gain (BMG) of incubating (red) and brooding (blue) king penguins in relation to foraging trip duration.

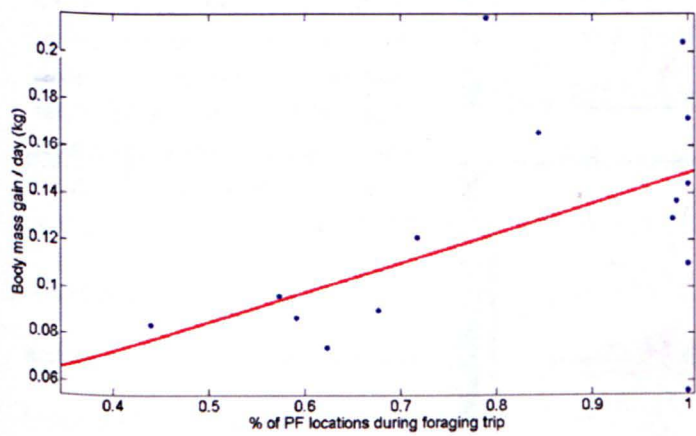


Figure 4.5: Daily body mass gain (BMG) of incubating king penguins in relation to the proportion of foraging locations in the Polar Front (PF). Frontal zones are defined by SSH signatures following Venables et al. (2012).

4.4.3 Frontal positions and water column structure in relation to bathymetry and frontal zones

During all study years, the SSH signature characteristic of the PF extended broadly across the Kerguelen Plateau and became more constrained and narrowed again further downstream to the east (Fig. 4.1). The SSH signature for the AAZ and SACCF followed the south-eastern edge of the Kerguelen Plateau along the 2000 m depth contour of the Fawn Trough canyon. After the Fawn Trough canyon the AAZ showed northward extensions of variable intensity over the Chun Spur to the eastern side of the Kerguelen plateau. The upper starting depth of the WW reached its shallowest depths at the sea surface along the south-eastern shelf break to the north and northwest of the Chun Spur in or close to AAZ waters (Fig. 4.6a). Cold WW in the water column explored by the penguins was restricted to areas to the northwest of the Chun Spur at depths greater than 1000 m (Fig. 4.6b).

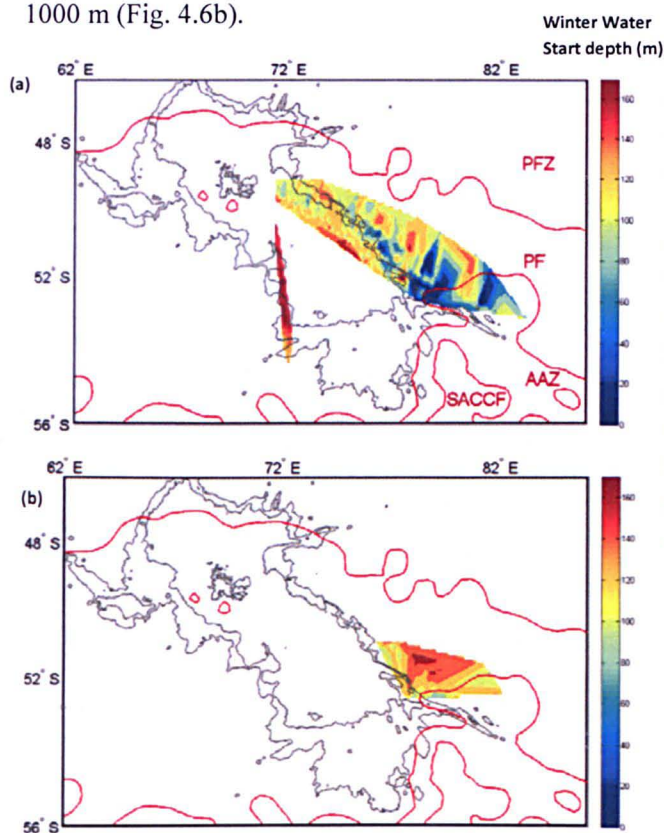


Figure 4.6: Maps of Winter Water (WW) start depth in the water column explored by incubating king penguins. a–WW (0.5–2°C), b–Cold WW (<0.5°C). Red contours indicate frontal positions from SSH signatures. Frontal positions on the maps are the mean positions over the trip period of all birds with Mk9 devices. PFZ: Polar Frontal Zone; PF: Polar Front; AAZ; Antarctic Zone; SACCF: Southern ACC Front.

4.4.4 Diving behaviour and water column exploration

Overall, incubating birds showed significantly shallower dive bottom start depths and lower dive efforts than brooding birds (Fig. 4.7).

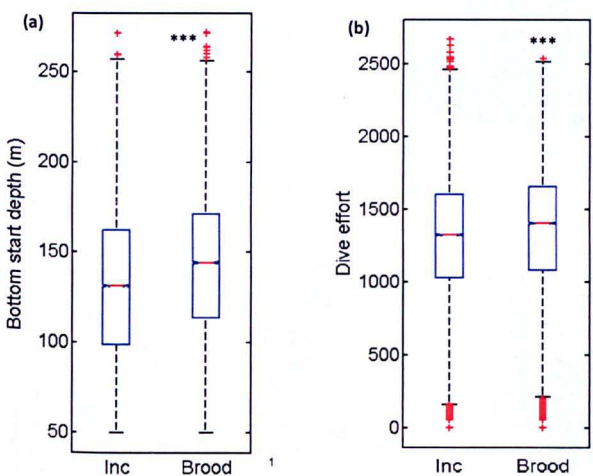


Figure 4.7: Differences in diving behaviour between incubating and brooding birds. a – Bottom start depth; b – Dive effort, calculated as the product of dive rate/h * bottom start depth. * indicate significant differences to the other breeding group with $p = 0.01$ (Kruskal-Wallis Test).**

4.4.4.1 Exploration of the water column during bottom periods in relation to bathymetry and frontal zones:

Incubating and brooding birds mostly explored the surface mixed layer (SML), the thermocline and WW during the bottom periods of their dives (Fig. 4.8a,b). The birds mostly targeted waters with weak negative temperature gradients $< -1^{\circ}\text{C} / 50\text{m}$, but some also explored stronger gradients of up to $-2^{\circ}\text{C} / 50\text{m}$. Incubating birds also explored positive gradients of up to $1^{\circ}\text{C} / 50\text{m}$ (Fig. 4.8a). Incubating birds spent similar proportions of their bottom periods in the SML and in WW (29.32 % and 37.54 %, respectively), whereas brooding birds spent more time in WW $<2^{\circ}\text{C}$ (52.66 %). CDW and cold WW accounted for 11.4% of the bottom periods of incubating birds, and CDW for 1.15% of brooding birds (Fig. 4.8b).

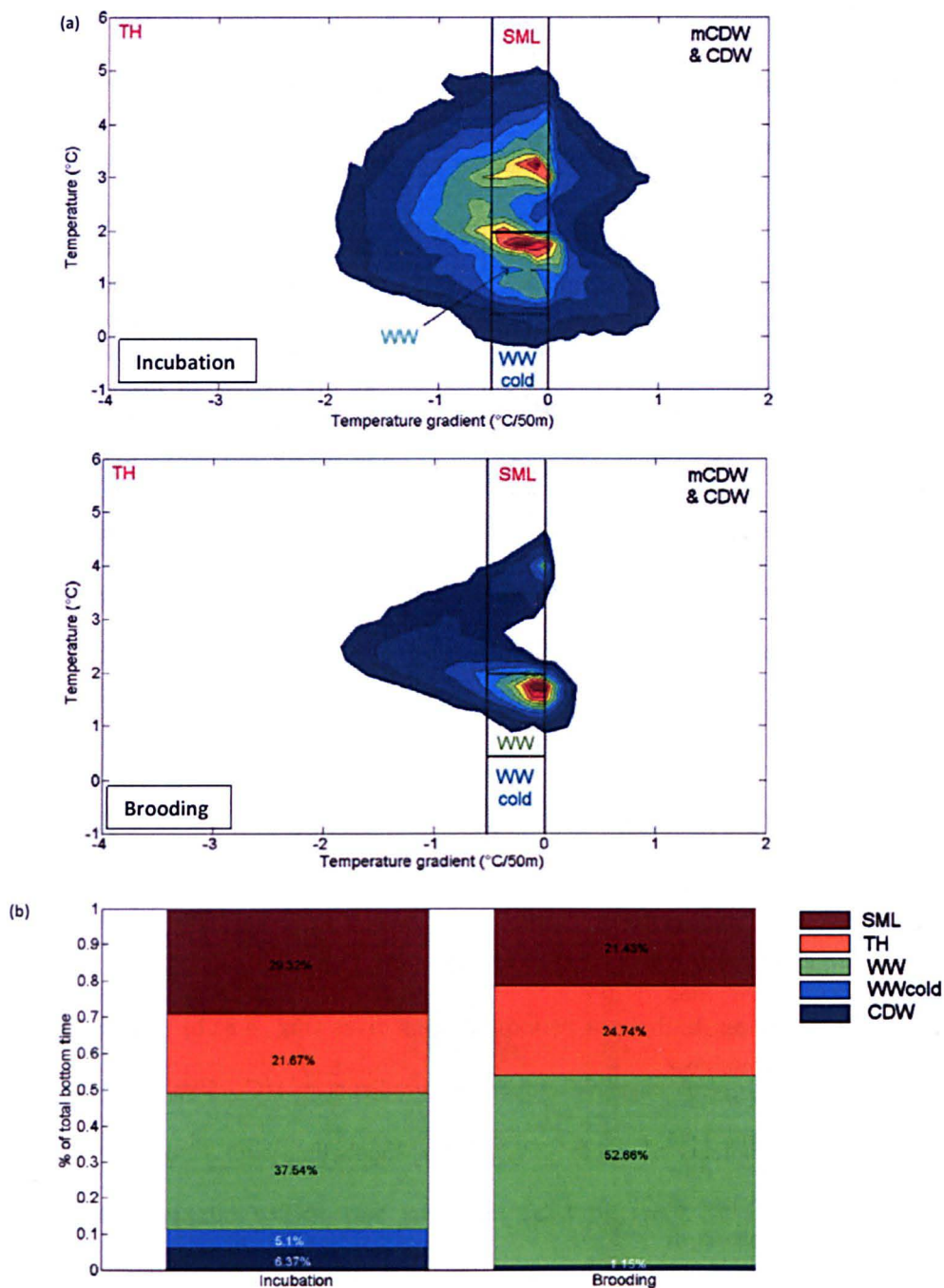


Figure 4.8: a - Thermal properties of the water column explored during bottom periods for incubating and brooding birds (only dives >50m). Contours encompass 5% and 10-90% of bottom time densities. b - Water masses explored during bottom periods for incubating and brooding birds (only dives >50m). Percentages represent proportions of the different water masses in relation to the total bottom time of the breeding group. SML-Surface Mixed Layer; TH-Thermocline; WW-Winter Water; WWcold-cold Winter Water <0.5°C; CDW-Circumpolar Deep Water; mCDW - modifiedCDW (Figure 4.8a only). For details of the water mass definitions see Material and Methods.

Water mass exploration during the bottom time of a dive changed with changing SSH and changing bathymetry (Fig. 4.9). Differences for incubating birds were most apparent with SSH (Fig. 4.9a) whereas there were only minor changes for incubating birds in relation to bathymetry (figure not shown). For brooding birds, water mass exploration during bottom times changed most with bathymetry (Fig. 4.9b). In general, the exploration of the SML during bottom time periods decreased and the WW exploration increased from the PFZ to the AAZ for incubating birds, and from shelf to offshore areas for brooding birds.

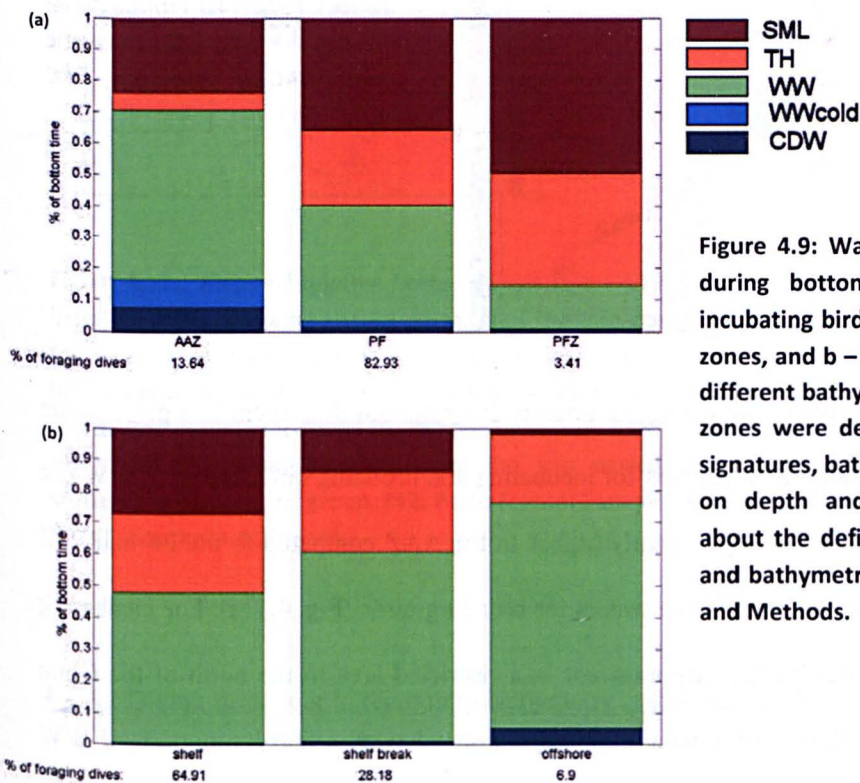


Figure 4.9: Water masses targeted during bottom periods a – for incubating birds in different frontal zones, and b – for brooding birds in different bathymetry zones. Frontal zones were defined based on SSH signatures, bathymetry zones based on depth and slope, For details about the definition of the frontal and bathymetry zones see Material and Methods.

The dive bottom start temperature decreased towards the south-east for incubating birds, with coldest temperatures occurring along the south-east shelf break of the Kerguelen Plateau and to the north of the Chun Spur (Fig. 4.10a). Brooding birds encountered their coldest bottom start temperatures in offshore waters to the SE of Kerguelen (Fig. 4.10b).

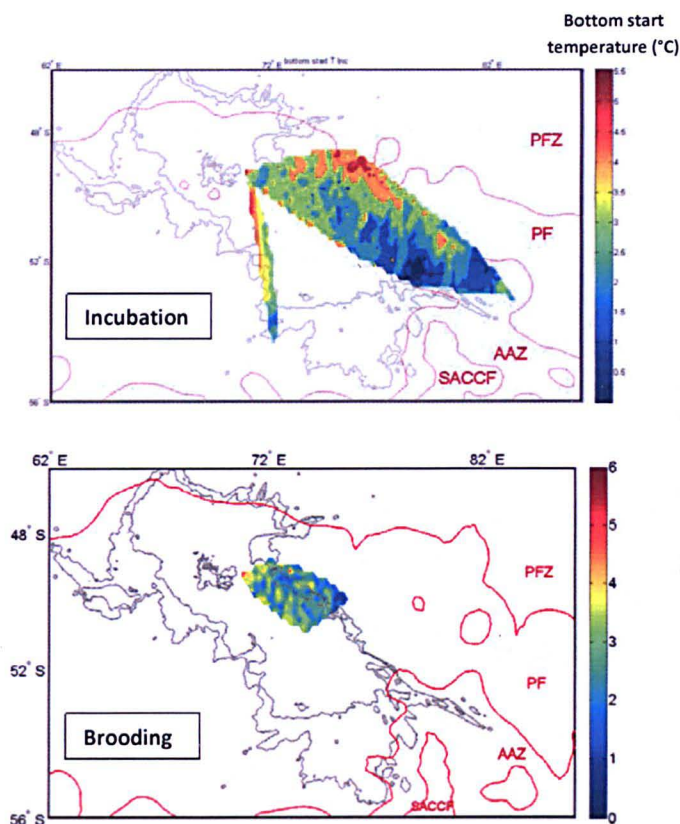


Figure 4.10: Maps of bottom start temperature of incubating and brooding birds. Grey contours show bathymetry at 0, 1000 & 2000m depth. Red contours indicate frontal positions from SSH signatures. Frontal positions on the maps are the mean positions over the trip period of all incubating and brooding birds with Mk9 devices. PFZ: Polar Frontal Zone; PF: Polar Front; AAZ: Antarctic Zone; SACCF: Southern ACC Front.

The relative bottom times, indicating the proportion of bottom time spent in a given water mass, showed distinct spatial patterns for incubating and brooding birds. Relative WW use during bottom periods was significantly higher in the AAZ compared to the PF and PFZ for incubating birds, and in offshore waters for brooding birds (Fig. 4.11a). For incubating birds, this pattern was particularly apparent in a restricted area to the north of the Chun Spur (51 to 53°S, 78 to 80°E), where bottom periods showed a high proportion of WW (Fig. 4.11a). CDW use during bottom periods for incubating birds occurred almost exclusively in a restricted area to the northeast of the Chun Spur in the AAZ, and only in very small proportions in the south easternmost offshore waters of the brooding birds foraging range (Fig. 4.11b).

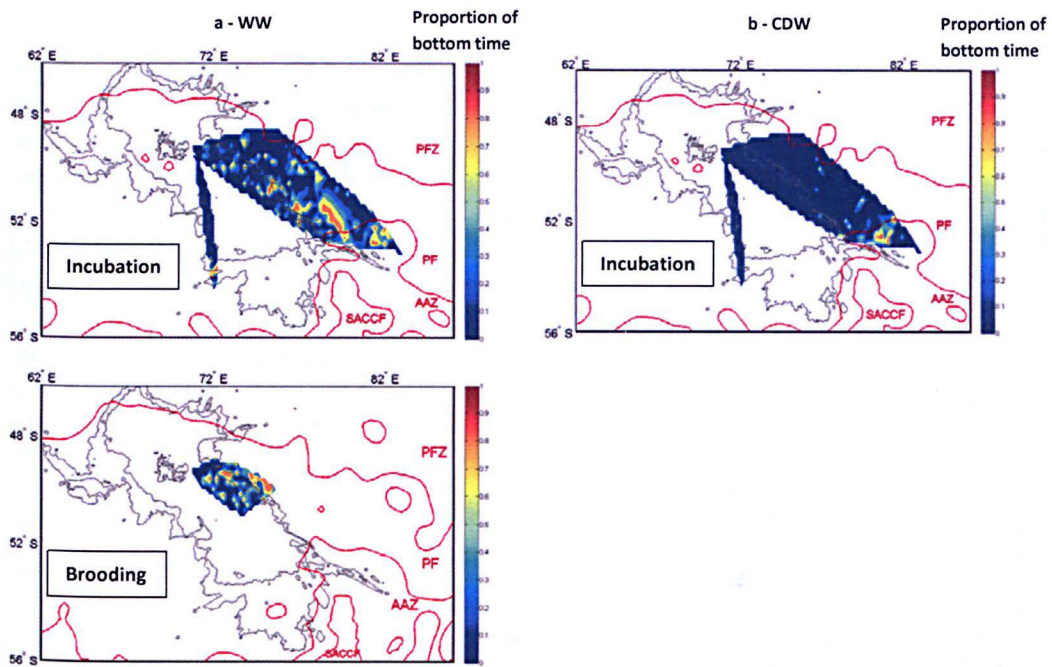


Figure 4.11: Maps of relative bottom times in a – WW and b - CDW for incubating and brooding birds, showing spatial patterns of the importance of the different water masses for foraging king penguins at Kerguelen. Coloured contours represent the proportion of bottom times spent in WW or CDW. Grey contours show bathymetry at 0, 1000 and 2000m depth. Red contours indicate frontal positions from SSH signatures. Frontal positions on the maps are the mean positions over the trip period of all birds included from the corresponding foraging group. PFZ: Polar Frontal Zone; PF: Polar Front; AAZ; Antarctic Zone; SACCF: Southern ACC Front.

4.4.4.2 Diving behaviour in relation to bathymetry and frontal zones:

Diving behaviour for incubating and brooding birds changed with different frontal and bathymetry zones (Fig. 4.12). The bottom start depths were shallowest in the PFZ for incubating birds and on the shelf for brooding birds, increasing towards AAZ and offshore waters. The dive efficiency was highest in the PFZ and on the shelf, and lowest in the AAZ and in offshore areas for incubating and brooding birds, respectively.

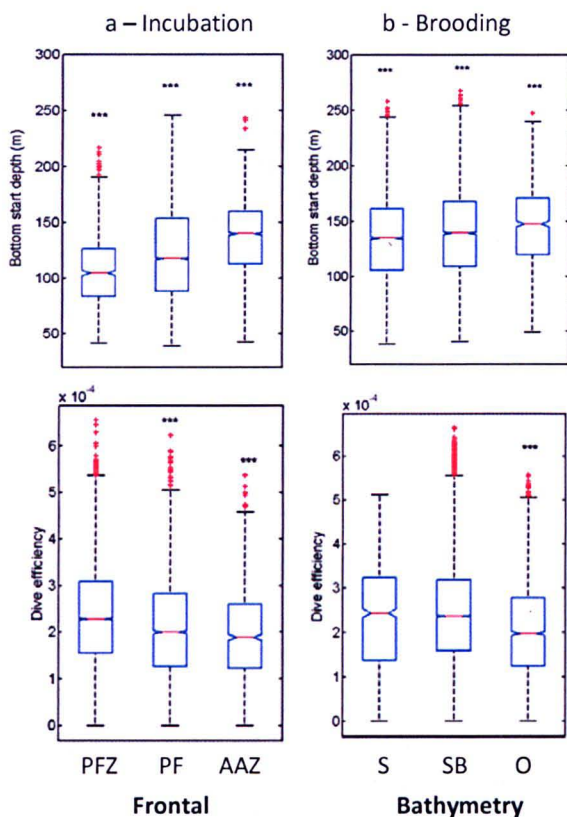


Figure 4.12: Changes in diving behaviour indicated by bottom start depth and dive efficiency with frontal and bathymetry zones. a – Incubating birds in different frontal zones; b – Brooding birds in different bathymetry zones. *** indicate significant differences to the other zones with $p = 0.01$ (Kruskal-Wallis Test). PFZ = Polar Frontal Zone; PF = Polar Front; AAZ = Antarctic Zone. S = shelf; SB = shelf break; O = offshore.

4.4.4.3 Diving behaviour in different water masses:

Diving behaviour showed differences depending upon which water masses were targeted during the bottom periods (Fig. 4.13). The broadness index and number of wiggles were highest during exploration of the thermocline for incubating and brooding birds. The dive efficiency and number of wiggles both showed significantly reduced values for both Cold WW and CDW compared with the SML, the thermocline and WW.

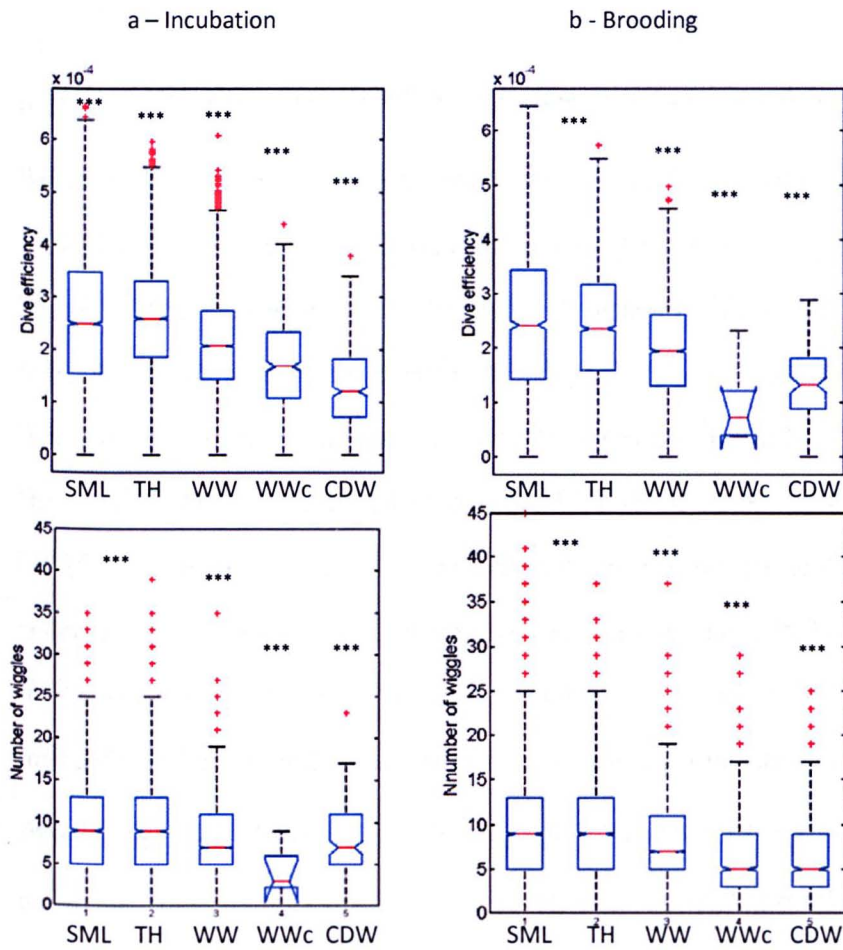


Figure 4.13: Foraging performance of king penguins in different water masses in terms of dive efficiency and wiggle numbers for a – incubating and b – brooding birds. *** indicate significant differences to the other water masses with $p = 0.01$ (Kruskal-Wallis Test). *** situated between two boxes indicate no significant differences between these two water masses, but with all the others. SML-Surface Mixed Layer; TH-Thermocline; WW-Winter Water; WWc-cold Winter Water <0.5C; CDW-Circumpolar Deep Water.

4.5 Discussion

4.5.1 Methodological discussion: Water masses definition through TDR data analysis

Evaluation of the thermal properties of the water column encountered by diving predators based on in-situ sampling is commonly used for the detailed study of their vertical habitat (Lydersen et al. 2002; Hooker & Boyd 2003; Biuw et al. 2007; Hooker et al. 2007; Costa et al. 2010). The use of TDR in-situ data only based on temperature values at foraging depth has been shown to be difficult, and may lead to controversial interpretations (McIntyre et al. 2011; Boersch-Supan et al. 2012). In this context it has been proposed to use water temperature at depth as a proxy variable for water mass (Boersch-Supan et al. 2012). In this study we defined different water masses based on the thermal properties of the water column encountered by the penguins. The interpretations of our results are therefore based on the exploration of different water masses, and behavioural changes may be related to shifts in water masses exploration, potentially reflecting oceanographic changes in the habitat explored by the animals.

Our definition of the different water masses is based on thermal properties of the water column and therefore simplified compared to classical oceanographic definitions based on temperature and salinity. Such definitions may be used if in-situ sampling by the animals includes salinity, as it can be the case for marine mammals (Costa et al. 2010). However, as TDRs attached to the penguins did not collect salinity data we based our definitions on temperature and temperature gradient, which reasonably reflected the important characteristics of the different water masses. As the results of this method showed accordance with visual inspection of thermal profiles as well as with general circulation patterns (Park et al. 2008b; Roquet et al. 2009; Roquet et al. 2010; Park & Vivier 2011) we assumed that our definitions were a realistic reflection of water column properties defining the different water masses.

We used static water mass definitions based on fixed temperature – temperature gradient values rather than dynamic definitions relative to the surrounding water column, such as the temperature minimum for Winter Water (WW) definition (Park et al. 2008b). This may impact the distinction of WW from Surface Mixed Layer (SML), as WW temperature can vary with latitude, and has been reported to reach temperature in the range of 2.6 – 0.5°C on the Northern Kerguelen Plateau (Park et al. 2008b). However, peaks of bottom periods in the temperature – temperature gradient plots occurred at thermal properties where water mass classification was unambiguous (clearly defined as SML or WW in temperatures below 2°C or above 3°C), and only a small proportion of bottom periods targeted water properties in the range of potential ambiguity between warm WW as SML (waters between 2 and 2.6°C) (see Fig. 4.8a). The implementation of a method based on dynamic water masses properties would have been more difficult, and our static method appeared to be sufficient for the purpose of our study.

Circumpolar Deep Water is usually defined by temperature-salinity properties, however, due to the temperature-only recording of the TDR sensors our water mass definitions were based on temperature and temperature gradient data only. While the spatial variability in CDW temperature makes its identification based on temperature-only data difficult, it may be clearly identifiable by the occurrence of positive temperature gradients in the water column at depths greater than 100 m from the signature of warm CDW below the cold WW. Such CDW identification based on the detection of positive temperature gradients in the water column >100 m allowed us to identify king penguins breeding at South Georgia and Kerguelen exploring CDW and modified CDW (mCDW) during their bottom periods.

4.5.2. Oceanographic patterns in the area to the south-east of Kerguelen

Frontal positions

The spatial patterns of the oceanography and frontal positions found in our study area were consistent with general circulation patterns in the Kerguelen area previously described in Orsi et al. 1995; Moore et al. 1999b; Sokolov & Rintoul 2009; Park et al. 2008b; Roquet et al. 2009; van Wijk et al. 2010; Park & Vivier 2011. However, the identification of frontal signatures associated with the Fawn Trough Current (FTC) showed important differences to those reported by Park et al. 2008b, Wijk et al. 2010 and Park & Vivier 2011, where waters assigned to the AAZ in our study were previously identified as the Southern ACC Front (SACCF) and the south PF, respectively. Such differences in oceanography and frontal locations between studies can occur and may be related to the fact that the definitions and property values for a given front may not be consistent all along its circumpolar path (Park et al. 1993; Belkin & Gordon 1996). This means that applying a static criterion validated in one location may lead to different results in other locations (Orsi et al. 1995; Park et al. 2008b). Complex circulation patterns resulting from interactions of oceanography with pronounced bathymetry, such as occur at the Fawn Trough are likely to amplify this effect, and increase apparent differences in frontal positions.

The Sea Surface Height (SSH) signatures used to define oceanographic features during our study were originally identified in the Scotia Sea, but were suggested to be valid for other parts of the Southern Ocean (Venables et al. 2012). Therefore, the identification of the Fawn Trough Current (FTC) as Antarctic Zone (AAZ) waters in our study may represent reconciliation with earlier assignments as the SACCF (Park et al. 2008) and the south PF (van Wijk et al. 2010) signatures, suggesting our frontal identification may be more correct. This is an important result for understanding the ecology of the Kerguelen Plateau.

Spatial patterns in water mass distribution and exploration by king penguins

Temperature data sampled by diving animals have been used for mapping oceanographic properties for a range of species and habitats (Charrassin et al. 2002; Charrasin et al. 2004; Lydersen et al. 2002; Hooker & Boyd 2003; Sokolov et al. 2006; Biuw et al. 2008; Costa et al. 2008; Costa et al. 2010). Such data facilitates the detailed mapping of oceanographic conditions within the water column at a fine spatial and temporal scale as it is encountered by animals; such mapping may not be possible using remotely sensed data or data from ship-based oceanographic transects (Hooker et al. 2007; Costa et al. 2010). Spatial patterns in water mass distribution encountered by our study penguins were consistent with circulation patterns reported in previous studies (Park et al. 1998; Park et al. 2008b; Charrassin et al. 2002; Charrassin et al. 2004; Roquet et al. 2009; Roquet et al. 2010; van Wijk et al. 2010; Park & Vivier 2011).

In our study, mapping the water column properties using a combination of TDR-Argos/GPS data allowed us to visualize fine-scale oceanographic patterns encountered by king penguins during their dives in agreement with Charrassin et al. (2004) who also used TDR data from free-ranging penguins. Furthermore our work reveals for the first time particularly small-scale interactions of oceanography with bathymetry downstream of the cold-water flow passing the Chun Spur. This allowed us to better understand spatial patterns in the oceanographic habitat explored by foraging marine predators such as king penguins, and to draw conclusions about relationships between the animals' foraging behaviour, oceanography and bathymetry.

Shallow Winter Water (WW) depths mapped by king penguins in our study were consistent with the cold-water flow along the south-eastern Kerguelen Plateau shelf break, as well as with areas of upwelling to the north of the Chun Spur and along the shelf break (Park et al. 2008b; Roquet et al. 2010; van Wijk et al. 2010). Mapping the temperatures at

the start of prey pursuit phases during the penguins' dives confirmed changes in oceanographic conditions in the water column induced by the cold-water subsurface flow, and showed the tracking of these changes by foraging king penguins during both incubation and brood.

Cold WW and Circumpolar Deep Water (CDW) occurrence in the water column explored by king penguins was limited to the area to the north of the Chun Spur in proximity to the AAZ northward loop over the Chun Spur, where the influx of the coldest waters of southern origins and the advection of upper CDW (UCDW) has been reported across the northern Chun Spur (Park et al. 2008b; Roquet et al. 2010). Interactions with bathymetry and other oceanographic processes in the area to the north of the Chun Spur may limit the occurrence of cold WW and CDW at depths available to king penguins. The UCDW layers reported by Roquet et al. (2010) are characterized by the deep T_{\max} layer situated at depths of 400 m. Other shallow, but infrequent, occurrences in our study may result from local upwellings or the exploration by king penguins of the boundary layer between WW and CDW.

4.5.3 General foraging trip patterns of king penguins at Kerguelen

Foraging trips for all birds were oriented to the south-east of the island, with significant differences in trip parameters between incubating and brooding birds. Incubating birds undertook extended foraging trips to the east and south-east of the Kerguelen Plateau, but mostly in proximity to the shelf break. Brooding birds undertook shorter trips, mainly foraging on the Kerguelen Plateau and on the shelf break to the south-east of Kerguelen. Such seasonal variation in foraging behaviour with reductions in trip duration after incubation is known to occur in many seabirds (Weimerskirch 2007), and especially in penguins that have limited travelling capacities. The variations are thought to be related to

the changing time constraints of the breeding cycle arising from the need to regularly feed the chick (Bost et al. 1997; Charrassin et al. 1999; Green et al. 2005). Changes in diving behaviour during brooding may reflect changes in prey pursuit behaviour, which might arise because different prey are targeted, and/or because prey requirements increase due to increased energy demand by the chick (Charrassin et al. 1999; Charrassin et al. 2002; Scheffer et al. 2012). Increased dive depths of brooding king penguins at Kerguelen indicate the target of deeper prey resources in the foraging areas close to the colony.

In other locations, similar patterns of reduction in foraging trip duration and changes in dive behaviour have been reported for king penguins during the brood stage. For example, at Crozet, both incubating and brooding birds target similar foraging areas, but considerably increase their travel speed and dive depths during brooding (Charrassin & Bost 2001; Charrassin et al. 2002), leading to higher travel and dive effort. At South Georgia, brooding king penguins undertake shorter foraging trips to closer foraging areas than during incubation, indicating less travel effort. However, some of the brooding penguins at South Georgia foraging closest to the colony dived to significantly greater depths and reduced the times at the bottom of the dives, indicating that these birds may reach their physiological dive limits (Halsey et al. 2010). At Kerguelen, short foraging trips with only a moderate increase in dive effort and constant proportions of bottom times during the dives occurred during brooding, indicating the presence of favourable foraging conditions in close proximity to the colony which appears to allow horizontal and vertical adaptations to increased time constraints without birds reaching their physiological limits.

4.5.4 Foraging behaviour in relation to oceanography

The consistent south-east orientation of foraging trips highlights the importance of these areas for foraging king penguins. The area to the south-east of Kerguelen is influenced by two major oceanographic features: the PF crossing the plateau just south of Kerguelen as it flows in a south-eastward direction along the east of the plateau, and the cold-water subsurface tongue of FT waters advected over the Chun Spur and flowing northwards along the eastern Kerguelen Plateau shelf break (Charrassin et al. 2004; Park et al. 2008b; Roquet 2010; Park & Vivier 2011). The area downstream of the Kerguelen Plateau is therefore characterized by high dynamics and strong thermal gradients arising from the convergence of the PF and the FTC driven by the bathymetric steering effect of the Kerguelen Plateau (Park et al. 2008b), as well as by high iron concentration arising from the island mass effect (Blain et al. 2001; Blain et al. 2007). Such conditions of high dynamics, strong thermal gradients and iron enrichment may lead to enhanced biological productivity (Lima et al. 2002) and the aggregation of higher trophic levels such as myctophids (Owen 1981; Schneider 1990), which may in turn impact upon the foraging behaviour of upper trophic level predators such as king penguins. Furthermore the cold waters of Antarctic origin may contain different myctophid resources (Duhamel 1998) making them accessible (both by latitude and depth) for king penguins following northward advection and upwelling at the Kerguelen Plateau. The cold-water subsurface tongue has been reported to be important for king penguins during brooding (Charrassin 2002, 2004), and may also be of importance for marine predators breeding at Heard Island (Wienecke & Robertson 2006; Hindell et al. 2011). Our study confirms the importance of this feature for king penguins at Kerguelen during the breeding season.

Role of the interaction between fronts, water masses and bathymetry for king penguins during incubation and brood

Incubating birds foraged along the south-eastern side of the Kerguelen Plateau between the shelf break and the PF as well as within the Chun Spur area. Exploration of the cold-water tongue from its origin at the Chun Spur until the latitude of Kerguelen during dive bottom periods suggests that strong foraging relationships exist with this feature. In the northern foraging areas in the PF and Polar Frontal Zone (PFZ), prey resources appeared to be associated with strong thermal gradients in the SML and thermocline (TH), which may be enhanced by the cold-water current meeting the south-eastward flow of the PF. Further to the south, foraging areas were concentrated over the area between the northern Chun Spur and the Heard-McDonalds Island Trough, where the penguins appeared to explore colder water masses for foraging. These locations have been shown to be important pathways of southern waters flowing onto the Kerguelen Plateau and into the area to the east of Kerguelen to form the cold-water subsurface tongue (Park et al. 2008b). Rugged bathymetry and seamounts may enhance upwelling of these cold waters, as indicated by shallow WW depths encountered by king penguins just upstream of the cold-water flow crossing the Chun Spur. Myctophids associated with the cold waters of Antarctic origin may thus become accessible to king penguins in such locations of enhanced upwelling, or aggregate at thermal gradients with warmer surrounding waters. Highest WW and CDW proportions, coldest water temperatures and the encounter of cold WW of Antarctic origin during bottom periods of the dives coincide with these areas of cold-water influx from the FTC, suggesting that birds may explore features related to such flows. Similar exploration of the cold-water influx over the shallow bathymetry in the Chun Spur area has been suggested for king penguins breeding at Heard Island (Wienecke & Robertson 2006), and may be important for other marine predators at Heard Island (king and macaroni penguins, black-browed albatrosses, and Antarctic fur seals) from the apparent coincidence of their

foraging locations with areas of the cold-water flow originating from the FTC (Hindell et al. 2011).

The foraging areas used by brooding birds were mainly located over the Kerguelen Plateau in the area between the PF and the subsurface cold-water tongue, corresponding to the trips made by brooding king penguins reported in Bost et al. (2002); Charrassin et al. (2002); Charrassin et al. (2004); Bost et al. (2011); Hindell et al. (2011). In this area, the subsurface cold-water current appears to be steered onto the shelf towards the island of Kerguelen (Charrassin et al. 2002; Charrassin et al. 2004), potentially by upwelling at the abrupt escarpment (between the 1000 to 3000 m isobaths) oriented in the north-south direction just to the east of Kerguelen (Charrassin et al. 2004). Such vertical flows of cold-water upwelling meeting with warmer PF waters over the plateau may generate strong thermal gradients at relatively shallow depths, where myctophids may aggregate. High levels of exploration of the SML and the thermocline during dive bottom periods indicate the target of prey resources associated with such vertical thermal gradients in shelf areas. The strongest mixing of water masses by internal tides at rather shallow depths of between 80 to 200 m (Mougin et al. 2008; Park et al. 2008a), corresponding to the depth of the majority of king penguins foraging dives, suggests the potential importance of these processes for prey aggregations targeted by king penguins. In shelf break and offshore waters, reduced levels of cold-water upwelling compared with shallow areas on the plateau as well as the northward loop of the PF over the shelf break to the east of Kerguelen may lead to reduced thermal gradients in the water column, as shown for areas east of 73°E (Charrassin et al. 2004). In these areas, the main prey aggregations explored by king penguins may be found in WW at greater depth, as indicated by cold dive bottom start temperatures and high proportions of WW during dive bottom periods. Antarctic fur seals breeding at Kerguelen which feed at moderate depths (less than 100m) also forage in similar areas to brooding king penguins (Lea & Dubroca 2003; Lea et al. 2008; Hindell et

al. 2011). This indicates the exploration of prey resources associated with similar processes.

Importance of the cold-water tongue and its variability for foraging king penguins

In summary, the subsurface cold-water flow originating from the FTC appears to play a key role for foraging king penguins during the incubation and brooding stage. The high intra- and interannual consistency in foraging trip orientation of brooding king penguins to the south-east of the island towards the shelf break and the classification of this area as an Area of Ecological Significance (AES) of the Kerguelen Plateau (Hindell et al. 2011) underline the importance of this area for king penguins and other marine predators breeding at Kerguelen. Similarly, the foraging areas of incubating king penguins also appear to exhibit a high level of spatial consistency close to the subsurface cold flow along the south-eastern shelf break. Foraging trip patterns for king penguins from Kerguelen shown in Hindell et al. (2011) suggest a similar orientation to the east and south-east of the plateau. However, these locations do not correspond to the Area of Ecological Significance identified by Hindell et al. (2011). Limited temporal coverage of the datasets, one year, used by Hindell et al. (2011) and any potential restriction in the level of sampling for different breeding stages may bias any AES identification; this may help explain why the foraging areas of incubating king penguins shown in our study are not included. Our study may therefore add information about areas of high significance for foraging king penguins, particularly during the incubation stage. These areas may also be of importance for other marine predators breeding on the Kerguelen Plateau, whose foraging areas also coincide with areas of the subsurface cold-water current close to its origin at the Chun Spur (Antarctic fur seals, macaroni and king penguins breeding at Heard Island), or with locations further upstream towards Kerguelen (black-browed albatrosses) (Hindell et al. 2011).

The opposing flow directions of the PF and the cold-water current together with their close proximity suggest that interactions exist between these oceanographic features. The PF is a major and deep-reaching ACC flow, and significantly stronger than the cold-water current. In consequence, variability in the PF position may have important impacts on the pathway and extent of the subsurface cold-water flow, and therefore the distribution of king penguins prey. King penguins are known to change foraging behaviour with variability in oceanographic features explored (Charrassin & Bost 2001; Péron et al. 2012), and may therefore adjust their foraging behaviour in relation to oceanographic conditions in the area to the east of Kerguelen. In this context, the PF position and its interaction with the subsurface cold-water current may play a key role. Most profitable areas closest to the colony (PF and PFZ for incubating birds, shelf area for brooding) may be targeted preferentially. If these areas do not provide sufficient prey resources, alternative foraging areas further away from the colony may be targeted (AAZ waters for incubation, shelf and offshore waters for brooding).

4.5.5 Importance of fronts and bathymetry for foraging king penguins at Kerguelen

Frontal zones and bathymetric features appear to play different roles in governing the foraging behaviour for king penguins of different breeding stages. Surface behaviour and water column exploration showed highest changes with frontal zones for incubating birds, whereas bathymetry appeared to play a more important role for behavioural changes of brooding birds. Such changes in foraging habitat exploration may reflect changing breeding constraints of central-place foragers such as king penguins, where foraging animals need to adapt their behaviour in order to exploit the best resources available within their changing constraints (Charrasin et al. 2002). Space and physical environment have been proposed to be best predictors of king penguins foraging habitat at Kerguelen (Bost et

al. 2011). During incubation, reduced time constraints may allow birds to explore more oceanic habitats with behavioural adaptations to large-and mesoscale oceanographic features, identified by SSH. During brooding, spatial restrictions due to regular provisioning of the chicks become more important, increasing the importance of the foraging habitat closer to the colony. Bathymetry, a prominent feature characterizing the habitat close to Kerguelen, is thus likely to play a more important role in foraging adjustments of brooding rather than incubating birds. While surface oceanographic parameters such as SSH and SST have been shown to play a role in habitat modelling of king penguins and other marine predators at Kerguelen (Bost et al. 2011; Hindell et al. 2011), their importance has been found to be relatively minor (Hindell et al. 2011). However, such relative importance of bathymetry-related or more oceanic processes appears to be impacted by the species biology and/or seasonal constraints. However, both incubating and brooding king penguins explored areas of cold-water upwelling at the Kerguelen Plateau where they changed diving behaviour to increased WW exploration during prey pursuit, suggesting the importance of such bathymetry-related processes for the species foraging. While such upwelling processes may be difficult to characterize by remotely sensed variables such as SSH and SST, our analysis of diving behaviour and water masses exploration shows the impact of changes in water column structure, presumably from upwelling, on the animals' behaviour.

4.5.5.1 Importance of the Polar Front (PF) area

The PF was the main foraging area for incubating and the exclusive foraging area for brooding birds. However, at Kerguelen, low travel times and associated energy costs for PF waters compared to other foraging areas are likely to play an important role in the foraging habitat choice of central place foragers such as king penguins. However, independent of spatial constraints, foraging dive performances for incubating birds were

significantly higher in the PF and PFZ compared with the AAZ, indicated by the shallow bottom start depths and high dive efficiency. Increasing body mass gains with the proportion of foraging spent in the PF confirms its importance for foraging king penguins in terms of overall foraging trip profitability. The PF is known to be a key foraging area for marine predators of the Southern Ocean (Bost et al. 2009), and has already been reported to play an important role for marine predators breeding at Kerguelen (Lea et al. 2002; Lea & Dubroca 2003; Lea et al. 2008). Myctophids, the main prey of king penguins (Olsson & North 1997; Bost et al. 2002), have been found to be highly accessible at the PF in terms of reduced depth and high densities (Sabourenkov 1991; Pakhomov et al. 1994), potentially due to their aggregative behaviour at the strong thermal gradients (Kozlov et al. 1991) arising from the juxtaposition of Antarctic and Subtropical water masses. In the area to the south-east of Kerguelen, such thermal gradients in the PF region may be enhanced by the northward deviation of cold Antarctic waters by the subsurface current. High use of the PF as a foraging area during incubation and brooding together with high foraging dive performances emphasize the importance of this oceanographic feature for foraging king penguins, confirming previous studies on king penguins breeding in other locations (Bost et al. 1997; Guinet et al. 1997; Sokolov et al. 2006; Trathan et al. 2008; Bost et al. 2009; Scheffer et al. 2010).

4.5.5.2 Importance of the Kerguelen Plateau for king penguins and their foraging adjustments

The Kerguelen Plateau provides an important foraging area for a number of marine predators such as Antarctic fur seals, black-browed albatrosses, southern elephant seals and penguins (Guinet et al. 2001; Lescroel & Bost 2005; Lea et al. 2008; Hindell et al. 2011). The interaction of the Plateau's bathymetry with oceanography is known to create stable and spatially delimited areas of high productivity (Mougin et al. 2008; Dragon et al. 2011;

Park & Vivier 2011), which may allow directed foraging trips to predictable resources as well as high levels of adaptation of foraging habitat exploration to seasonal constraints, as indicated by the clear foraging habitat segregation of incubating and brooding birds. This may be of particular importance for animals under high energetic constraints, as it provides reliable foraging areas close to the colony. In our study, brooding birds exploring these areas were able to reduce their travel distances as well as increasing their dive depths only moderately. At Kerguelen, predictable prey resources at relatively shallow depths close to the colony appear to allow king penguins to adapt foraging to increased breeding constraints without increasing surface travel, and with only moderate increases in dive effort. This may also be the case for other marine predators exploring similar areas for foraging (Hindell et al. 2011).

However, these prey resources over the Kerguelen Plateau shelf in proximity of the breeding colonies may be of increased temporal and spatial small-scale variability due to enhanced vertical mixing by tidal forces (Mongin et al. 2008; Park et al. 2008a) and the lack of aggregative effects of pronounced oceanographic features over the plateau between the PF and the FTC (Park et al. 2008b), leading to reduced stability and therefore reduced overall profitability of these prey resources. High daily body mass gains (BMG) for short foraging trips but with a rapid decrease in BMG with increasing trip duration suggests that prey resources may allow profitable foraging for relatively short periods, but may be less profitable for longer trips. Deeper dives with longer bottom periods for brooding birds may indicate such exploration of less favourable prey conditions (Charrassin et al. 2002; Halsey et al. 2010) at greater depths and requiring longer pursuit times at the bottom of the dives in shelf areas. Marine predators with lesser time constraints may target areas of higher large- and mesoscale activity in proximity of the Kerguelen Plateau, as shown by incubating king penguins. In these areas, the combined effect of bathymetry-related processes such as upwelling and channelling of ACC flows, and of structuring effects of

large-and mesoscale oceanographic features on the marine environment and prey resources may create patches of higher stability and density. This may provide more favourable foraging conditions for marine predators under lesser time constraints such as incubating king penguins, which are able to spend more time exploring more distant and more extensive foraging areas for profitable prey resources (Bost et al. 1997; Guinet et al. 1997; Trathan et al. 2008; Scheffer et al. 2010). Similar foraging trip orientations for Antarctic fur seals breeding at Kerguelen either over the shelf to the south-east of the island or in offshore waters to the east of Kerguelen (Lea & Dubroca 2003; Lea et al. 2008) indicate similar behavioural patterns for other marine predators at Kerguelen. However, there was no information on differences in breeding stages of the animals targeting these different foraging areas. Both types of foraging habitat, bathymetry-related upwellings on the shelf or the shelf break as well as oceanic processes in offshore areas appear to be of major importance for marine predators breeding at Kerguelen, where the importance may depend on the species biology and seasonal constraints. Our study therefore confirms the importance of AES on the Kerguelen Plateau shelf identified by Hindell et al. (2011), but also suggests the importance of offshore areas with mesoscale features related to the PF and its juxtaposition with the cold-water current to the south-east of Kerguelen, at least to less constrained animals.

4.5.6 Diving behaviour in different water masses

King penguin foraging performance changed with the water mass targeted during the bottom periods of the dives. Heterogeneity in myctophid distribution in the water column is thought to be related to species, depth and physical properties of the water column (Hulley 1981; Collins et al. 2008, 2012). Therefore, different water masses host prey resources of different species composition and patch properties (Hulley 1981; Kozlov et al.

1991; Pusch et al. 2003; Collins et al. 2008; Collins et al. 2012), which is thought to impact foraging behaviour and performance of diving predators such as king penguins (Bost et al. 2002). The foraging performance of a dive is further impacted by the travelling time through the water column to reach the prey resources (Wilson 1995). The targeting of deeper water masses increases travel time through the water column and reduces the time available for prey pursuit at depth, therewith decreasing foraging performance if homogeneity in prey distribution in the water column is assumed. Foraging performance associated with a given water mass is therefore a combination of depth and the profitability of associated prey resources together with the distance from the colony.

King penguins at Kerguelen appeared to encounter most favourable foraging conditions in the thermocline, indicated by the highest dive efficiency and wiggle numbers. Wiggles during the bottom period have been shown to reliably identify prey catch events in king penguins (Bost et al. 2007; Hanuise et al. 2010), and have therefore been used as proxies for feeding success. The thermocline is the layer of one of the most pronounced thermal gradients in the ocean, resulting from the juxtaposition of warm SML and cold WW. It is known to be a location of enhanced biological activity (Weston 1953; Sameoto et al. 1986; Hunt 1990), resulting in the accumulation of biomass for various trophic levels, ranging from planktonic organisms to mesopelagic fish and ultimately upper trophic level predators (Hunt 1990; Spear et al. 2001). This is particularly the case for myctophids, king penguins main prey, these are known to aggregate at strong thermal gradients (Hulley 1981; Kozlov et al. 1991; Pakomohov et al. 1996) such as the thermocline. The thermocline may therefore host dense myctophid aggregations at relatively shallow depths, allowing highly efficient foraging with high proportions of dive time available for bottom periods when targeting these prey resources. The importance of the thermocline has already been reported for king penguins in other locations, where birds target prey associated with or close to thermal discontinuities in the water column at Crozet

(Charrassin & Bost 2001) and South Georgia (Scheffer et al. 2012). This study confirms the key importance of the thermocline for foraging king penguins at Kerguelen, as important proportions of the underwater foraging phases (bottom phases) occurred in the thermocline.

Decreased diving performance during dives to deeper water masses would result in reduced times available for prey pursuit, suggesting that king penguins may preferentially target the thermocline, SML and WW. However, CDW and mCDW may host different prey species or different prey distributions (Pusch et al. 2003; Collins et al. 2012), and may therefore represent important foraging habitats for king penguins especially if they locate insufficient prey resources at shallow depths. At South Georgia, brooding king penguins foraging close to the colony have been reported to consistently target CDW during dive bottom periods, resulting in high BMG from only short bottom periods (Scheffer et al. 2012). This suggests that CDW may host profitable prey resources in the region close to South Georgia. Prey resources associated with deeper or more southerly water masses, such as CDW or cold WW, may represent important alternatives when shallow prey is insufficient during periods of increased resource demand (e.g. during breeding), or resulting from when environmental factors impact prey distribution. However, profitability of prey resources associated with CDW may be related to local oceanography. At South Georgia, CDW appears to provide an important foraging niche in areas closest to the colony for birds under high breeding constraints, whereas king penguins breeding at Kerguelen targeted CDW almost exclusively during incubation in areas distant from the colony.

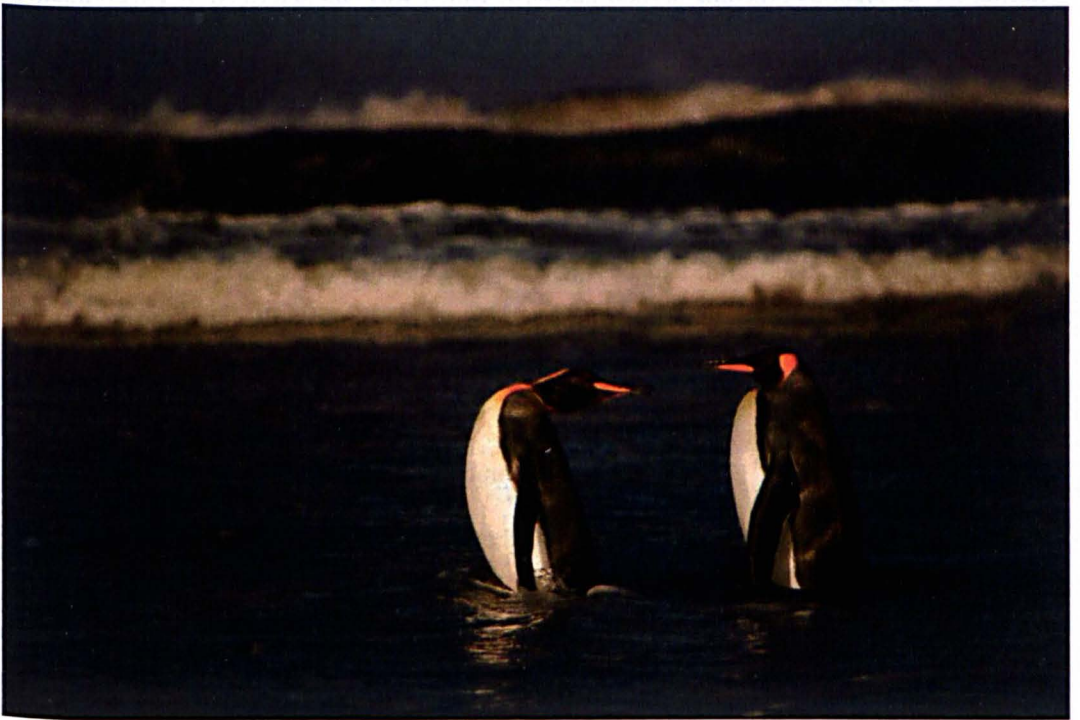
The exploration of different water column properties and different water masses has already been reported for king penguins and other diving predators (Charrassin & Bost 2001; Lea & Dubroca 2003; Biuw et al. 2007; Biuw et al. 2010; Lea et al. 2008; Trathan et

al. 2008; Muelbert et al. 2012; Scheffer et al. 2012), showing the non-random exploration of the vertical hydrological habitat by animals and the impact of thermal properties of the ocean on their foraging behaviour. Our study confirms these findings for king penguins breeding at Kerguelen, and furthermore identifies changes in foraging dive performances in different water masses.

Chapter 5

The particular situation in 2009/10 -

**An exceptionally bad year for king penguins breeding at
Kerguelen**



5.1 Abstract

Flexibility in foraging behaviour allows marine predators to buffer reproductive success against variability in environmental conditions and prey availability by allocating more time to foraging when food density decreases. However, such adaptive capacities are limited by thresholds in environmental conditions governing prey availability, beyond which the animals are not able for such buffering anymore, leading to reproductive failure due to insufficient provisioning. Investigating such thresholds is of key importance for a better understanding of the animals' abilities to adapt to environmental variability.

In this study we examined the foraging behaviour of king penguins breeding at Kerguelen during the anomalous breeding season 2009/10, which was characterized by exceptionally long foraging trips and low reproductive success. We used Argos and Global Positioning System (GPS) tracking together with Time-Depth-Temperature Recorders (TDR) to follow the at-sea movements of the penguins. Combining the penguins' behaviour with oceanographic data from remote sensing as well as from the in-situ recordings by the penguins allowed us to relate the observed behavioural anomalies to oceanographic anomalies in the foraging area.

Extended foraging trips beyond the usual foraging range of other years as well as significantly altered dive characteristics and the manner in which penguins utilised the thermal structure of the water column in 2009/10 suggests that the local oceanography and associated prey field may have been strongly altered in such a way that king penguins were not able to forage successfully in their usual foraging area. Southward shifts in key oceanographic features present in the penguins' foraging area as well as the disruption of the thermal structure of the water column led to significant changes in oceanography (and the associated prey distribution) following fluctuations in regional climatic drivers.

Our results indicate that the capacity of king penguins to adapt to variability in oceanographic conditions and associated prey resources in their foraging area may be limited; 2009/10 reflected changes in the environment beyond which successful foraging and reproduction was significantly impacted. The breeding season 2009/10 may therefore allow us to identify key environmental conditions and environmental thresholds for successful foraging and reproduction at Kerguelen, which will be important in the context of regional climate change.

5.2 Introduction

The ability of animals to adjust their foraging behaviour plays a crucial role in their survival and reproduction, buffering reproductive success against variability in resource availability. In the marine environment, environmental variability impacts upon oceanographic conditions and the horizontal and vertical distribution of the different water masses (Solomon et al. 2007; Doney et al. 2012), and therefore upon the distribution of prey for marine predators. Flexibility in foraging behaviour is therefore a crucial part of the survival and reproduction of marine predators.

However, the reproductive output of marine predators is known to be affected by environmental variability (Weimerskirch et al. 2003; Jenouvrier et al. 2005; Murphy et al. 2007a; Trathan et al. 2007; Forcada & Trathan 2009; Costa et al. 2010; Barbraud et al. 2011; Péron et al. 2012), suggesting that thresholds may exist where foraging flexibility can no longer buffer reproductive success against low food availability (Dall & Boyd 2002). Marine predators have been shown to exhibit threshold-type responses to changes in prey availability, where small changes in prey can trigger rapid and non-linear changes in foraging effort, reproductive performance and/or adult survivorship (Cairns 1987; Reid et al. 2005; Harding et al. 2007; Piatt et al. 2007; Raconi & Burger 2008). Identifying and

investigating environmental conditions leading to such threshold situations is crucial to improve our understanding of how the animals explore their environment, and how they may respond to potential future environmental change.

Environmental variability may occur across different temporal and spatial scales, ranging from large-scale sub-decadal signals such as the El Niño-Southern Oscillation (ENSO) or Southern Annular Mode (SAM) to small-scale weekly or daily events such as local atmospheric anomalies. While larger-scale oscillating signals such as ENSO and SAM as well as general global trends such as ocean warming have been shown to significantly impact marine predators in the Southern Ocean (Croxall et al. 2002; Vargas et al. 2006; Trathan et al. 2007; Forcada & Trathan 2009; Ainley et al. 2010), the impacts of smaller-scale variability or their potential local amplification effect on larger-scale signals (Paine et al. 1998; Meehl et al. 2000) are less well understood.

In the context of environmental variability, ecosystems or ecosystem components may undergo extreme events, which are characterized by their statistical extremity and by the abruptness relative to the life cycle of the organisms affected (Jentsch et al. 2007). Extreme events have the potential to allow insights into reactions of ecosystems or specific components to extreme conditions, which may indicate potential reactions and adaptations to future environmental change (Trathan et al. 2007; Forcada & Trathan 2009; Péron et al. 2012). Ongoing climate change and future warming of the oceans (Gille 2002; Solomon et al. 2009) means extreme events are predicted to be more frequent (Jentsch et al. 2007; Solomon et al. 2007; Jentsch & Beierkuhnlein 2008), suggesting that event-based approaches to extreme events may be necessary in addition to trend-based research (Jentsch et al. 2007). Such approaches of the detailed study of extreme events may give indications about if and how to incorporate environmental key parameters into modelling

studies of predators' foraging behaviour, and may improve our abilities of predicting potential impacts of future environmental change on marine predators..

King penguins are important avian predators of the Southern Ocean (Woehler 1995; Bost et al. 2012). They feed mainly on myctophids (Myctophidae: lantern fish) (Cherel & Ridoux 1992), mesopelagic fish that are generally associated with particular water masses or temperature ranges (Hulley 1981; Kozlov et al. 1991) as well as with fronts and related oceanographic features (Brandt et al. 1981; Pakhomov et al. 1996; Rodhouse et al. 1996). The horizontal and vertical distribution of water masses is therefore of key importance for foraging predators such as king penguins. King penguins are known to dynamically adapt their foraging behaviour to the conditions encountered (Charrassin et al. 2002), allowing buffering foraging and reproductive success against variability in oceanography and associated prey resources in the foraging area. During the summer breeding season, king penguins undergo important time and energy constraints, as the parents take turns to incubate the egg or brood the young chick (Charrassin et al. 1998, 2002; Halsey et al. 2010), thus undergoing prolonged periods of fasting ashore while their partner is foraging at sea (Stonehouse 1960; Groscolas 1990). Depletion of the adult's body reserves may lead to breeding failure, where parents may sometimes abandon their egg or chick and return to forage at sea before their partner's return to the colony (Olsson 1997; Groscolas et al. 2000; Gauthier-Clerc et al. 2001; Olsson & van der Jeugd 2002).

The Kerguelen archipelago is situated on the extensive Kerguelen Plateau in the south Indian Ocean. Acting as a major bathymetric obstruction in the eastward flow of the Antarctic Circumpolar Current (ACC), the Kerguelen Plateau plays a significant role in the steering and channelling of most of the deep-reaching ACC flow (Park et al. 2008b; Sokolov & Rintoul 2009; Park & Vivier 2011). The most prominent oceanographic features in the area to the south-east of Kerguelen are the Polar Front (PF) and the Fawn

Trough Current (FTC), both of which are part of the ACC. The PF has been identified to flow eastwards across the northern Kerguelen Plateau just south of Kerguelen (Park et al. 1998; Charrassin et al. 2004; Park et al. 2008b, Park & Vivier 2011), then wraps anticyclonically around the island from the south-east to continue its flow north-eastward, and then flows again south-eastwards along the east of the Kerguelen Plateau (Park & Vivier 2011). The FTC is a strong current flowing along the southern edge of the Northern Kerguelen Plateau through the Fawn Trough, a deep passage (<2800 m) separating the Southern and the Northern Kerguelen Plateau and channelling an important part of the ACC flow (Park et al. 2008b; Roquet et al. 2009). The cold waters advected from the Fawn Trough over the Chun Spur flows northwards along the eastern shelf break of the Kerguelen Plateau, forming a cold-water subsurface tongue that can extend up to the latitude of Kerguelen (Charrassin et al. 2004; Park et al. 2008b; van Wijk et al. 2010), where it reaches depths of ~100 m (Charrassin et al. 2004). Its northward extension appears to be variable, but the factors affecting the flow are not well understood.

King penguins are one of the most important avian predators breeding at Kerguelen (Bost et al. 2012), comprising an estimated 342 000 breeding pairs, quickly increasing (Chamaillé-Jammes et al. 2000; Bost et al. 2012, last estimate dating to 1999). During the summer season, king penguins generally explore the area to the south-east of Kerguelen during their incubation, brooding and crèche foraging trips (see Chapter 4; Koudil et al. 2000; Charrassin et al. 2002; Bost et al. 2002; Pütz et al. 2002; Charrassin et al. 2004; Bost et al. 2011; Hindell et al. 2011), where the subsurface tongue of cold water originating from the FTC and its juxtaposition with the PF have been shown to be of key importance for the foraging penguins (see Chapter 4; Charrassin et al. 2002; Charrassin et al. 2004). However, there is currently no knowledge about how penguins may adapt to changes in these key oceanographic features, and what may be their limits of flexibility in foraging behaviour to buffer such variability.

Records of exceptionally low reproductive success and/or anomalous foraging behaviour of king penguins (Gauthier-Clerc et al. 2001; Olsson & van der Jeugd 2002) and other marine predators of the Southern Ocean (Hill et al. 2009) may indicate that certain environmental conditions governing prey availability and distribution were beyond the range of the penguins' adaptive capacities to buffer reproductive success against environmental variability. Investigating such environmental thresholds impacting foraging flexibility may improve our knowledge of the foraging behaviour of king penguins, help identifying environmental key features triggering such threshold situations as well as improve our capacities to assess potential consequences of future environmental changes.

In this study we investigated the foraging behaviour of incubating king penguins breeding at Kerguelen during one year of unprecedented anomalies in the bird's foraging and reproductive success. We identified anomalies in surface and diving behaviour from Argos/GPS and TDR data, and related such behaviour to oceanographic anomalies regarding the PF position and the influx of FTC waters into the penguins' foraging area. We further looked at changes in horizontal and vertical foraging habitat exploration in terms of surface features and specific water masses at depth in response to changes in the oceanographic habitat. Carrying out such detailed analysis of one particular season enabled us to study the penguins' reactions to extreme environmental conditions, to identify oceanographic features in the horizontal and vertical dimension that may be crucial for the penguins' successful foraging, and to identify potential thresholds in local oceanography beyond which king penguins breeding at Kerguelen may lose their adaptive capacities of buffering reproductive success against environmental conditions.

5.3 Material and Methods 2

5.3.1 Study area, study period and device deployments

Study area, study period and device deployments correspond to those described in Chapter 4.

5.3.2 Environmental data

Environmental data used (bathymetry and slope as well as vertical temperature data and water mass definition from the TDR data) correspond to those described in Chapter 4. In addition to the data in Chapter 4 we used the following remotely sensed oceanographic data:

a - Sea surface temperature (SST) and SST anomaly (SSTA) data: We used two different SST/SSTA datasets of different spatial and temporal resolution depending on the scales of oceanographic processes considered. 1 - For the visualization of oceanographic processes at small spatial and/or temporal scales as well as for the determination of SST/STTA encountered by the penguins over their foraging trip we used OSTIA (Operational Sea Surface Temperature and Sea Ice Analysis) SST and SSTA data from The Met Office (FitzRoy Road, Exeter, UK). OSTIA provides gap-free foundation SST values, SST_{nd}, defined as the temperature of the water column free of diurnal temperature variability (daytime warming or nocturnal cooling) from interpolation of satellite and in-situ data. Data were available at a spatial resolution of 0.05° (SST) and 0.25° (SSTA) with a daily temporal resolution. Daily SSTA data represent anomalies relative to the mean daily SST during 1998 – 2009. More details about OSTIA are available at http://ghrsst-pp.metoffice.com/pages/latest_analysis/ostia.html. 2 - For the visualisation of global or basin-wide SST and SSTA patterns at monthly scales we used SST data from the Met Office Hadley Centre observations sea ice and sea surface temperature (HadISST1) dataset

(available through the BAS database) at a temporal resolution of 1 month. Monthly SSTA data are relative to the mean monthly SST during 1950 – 2011. More details about the HadISST1 dataset are available on <http://www.metoffice.gov.uk/hadobs/hadisst/>.

b - Sea surface height (SSH) data: We used absolute dynamic topography (ADT) Delayed time (DT) data from Aviso (www.aviso.oceanobs.com). Data were available at a spatial resolution of $1/3^\circ \times 1/3^\circ$ and a weekly temporal resolution. ACC fronts and zones were defined based on SSH signatures following Venables et al. (2012). These frontal signatures were defined based on the Scotia Sea, but are stated to be valid for other locations of the Southern Ocean (Venables et al. 2012).

c - Geostrophic velocity data: We downloaded geostrophic velocity data from Aviso (www.aviso.oceanobs.com). Geostrophic velocities arise from the balance between horizontal gradients in Sea Surface Height (SSH) and the Coriolis Force, indicating the strength and direction of an ocean current. Geostrophic velocity data were available at a spatial resolution of $1/3^\circ \times 1/3^\circ$ and a weekly temporal resolution.

d - Atmospheric and sea-ice data

Mean Sea Level Pressure (MSLP) and wind data climatologies and anomaly composites were downloaded from the National Oceanic and Atmospheric Administration (NOAA) Earth System Research Laboratory and National Centers for Environmental Prediction (NCEP).

Sea-ice anomaly data for the south Indian Ocean during August and September 2009 were obtained from the Met Office Hadley Centre observations sea ice and sea surface temperature (HadISST1) dataset (available through the BAS database). More details about the HadISST1 dataset are available on <http://www.metoffice.gov.uk/hadobs/hadisst/>.

5.3.3 Data analysis:

5.3.3.1 Analysis of surface behaviour

Processing of the Argos and GPS data was carried out as described in Chapter 4, using the process model of state space models for the Argos data. First-passage time analysis was applied to the surface tracking data to identify foraging behaviour (see Chapter 4 for a more detailed description). For each location we assigned Ostia SST, SSH, geostrophic velocity, bathymetry and slope values by searching for the geographically nearest value within the corresponding dataset.

For each bird, we calculated trip duration, distance covered, maximum distance from the colony and the furthest latitude south and east reached. Exact departure and return times from and to the island from field observations where possible, and from visual inspection of surface tracks arriving at the colony.

5.3.3.2 Analysis of diving behaviour

A zero offset correction was applied on the dive data. Only dives deeper than 50 m depth were used for analysis, as they were considered to represent the majority of king penguins foraging dives (Pütz et al. 1998; Charrassin et al. 2002).

Diving behaviour was analysed by calculating the following dive parameters: duration and start depth of the bottom phase (the time between the first and last wiggle or dive step deeper than 75% of the maximum dive depth, following Halsey et al. 2007), the number of wiggles (deviations >1 m of depth with an absolute vertical instant greater than 0) as a reliable proxy of feeding success (Bost et al. 2007; Hanuise et al. 2010). Furthermore, we determined the dive efficiency (DE), calculated as bottom duration / (dive duration + post-dive interval) following Ydenberg & Clark 1989. We also determined the product of dive rate \times bottom start depth as an indicator for the physiological effort due to diving activity,

where dive rate was calculated as the number of dives $>50\text{m}$ carried out in an ± 30 minutes interval around each dive. The relative bottom time spent in a specific water mass was calculated as the proportion of the total bottom time of the dives spent in the particular water mass. This allowed the evaluation of the importance of a water mass for prey pursuit. The foraging profitability of the different water masses was defined on the cumulative number of wiggles, indicating the importance of the different water masses for prey pursuit.

Vertical profiles of diving behaviour and in-situ thermal properties of the water column were calculated as described in Chapter 4. TDR temperature recordings at 10 m depth during the ascent phase of the dives were assigned to each dive as an approximation of SST after checking for correspondence to Ostia SST foundation values. This allowed for assigning SST values to TDR data from birds without Argos/GPS recordings, as there were no combined TDR-Argos/GPS data in that year.

As king penguins are visual feeders and essentially forage during the daylight and twilight hours (Bost et al. 2002), night dives were excluded from these analyses (corresponding to 16.7% of the total dives < 50 m depth, and 2.1% of the total dives > 50 m depth). However, in 2010 no combined TDR – GPS data was available, as birds equipped with both device types could not be identified to be returned back to the colony due to exceptionally extended foraging trips and therefore unknown return dates to the colony. Therefore geographical coordinates of the dives could not be calculated, and the interpolation of horizontal environmental parameters (oceanographic and bathymetric) for the dives as well as the calculation of exact sunrise and sunset times were impossible. For the approximate identification of sunrise and sunset, and the consequent discharge of night dives from the analysis, we used the sunrise time at the easternmost and sunset time at the westernmost point reached by the foraging trips in 2010. This method allowed to exclude

night dives from the analysis while being conservative for twilight hours, leading to including some night dives into the analysis instead of possibly discharging twilight dives if sunrise and sunset times were set too late or early, respectively.

Comparisons of dive parameters between 2010 and other years were carried out using Kruskal-Wallis tests as tests for normality failed (Jarque Bera test) and transformations did not help the data to conform to the normality assumption. When significant differences were found among groups, an all pairwise multiple comparison (Dunn's method) was performed to determine the groups that differed from the others.

5.3.3.3 Analysis of changes in horizontal and vertical foraging habitat use

Detailed use of the water column by the penguins while foraging was analysed by considering the bottom phase and wiggle numbers of the dives, as the bottom phase is thought to be the most important phase for prey capture (Charrassin et al. 2002, Simeone & Wilson 2003; Ropert-Coudert et al. 2006), and wiggles have been shown to be reliable indicators of prey capture by king penguins (Simeone & Wilson 2003; Takahashi et al. 2004; Bost et al. 2007; Hanuise et al. 2010). Bottom periods were analysed by considering temperature, temperature gradient and the water masses encountered.

Changes in horizontal and vertical foraging habitat use were analyzed regarding SSH and geostrophic velocities of foraging locations, and temperature and temperature gradient (and consequently the exploration of different water masses) during bottom periods of dives >50 m. Contour plots of foraging locations on SSH and geostrophic velocity axes, and of bottom periods on temperature and temperature gradient axes, allowed us to identify the target of oceanographic properties at the surface, and of thermal properties at depth during foraging. To determine changes in habitat use during a particular year compared to the

other years, habitat use densities were converted to gridcells, then normalized for the particular year as well as for the other years and then subtracted. Contour plots of the resulting distributions showed the relative differences in habitat use between the particular year and the other years.

5.3.3.4 Analysis of oceanographic data: Spatial and temporal patterns of oceanographic conditions in the area to the south-east of Kerguelen, and potential anomalies during the austral summer 2009/10

From the Ostia SST and Aviso SSH data we assessed the fine-scale structure of the horizontal and vertical habitat in the foraging area explored by king penguins. This allowed us to investigate detailed relations of the penguins' foraging behaviour with oceanographic conditions at the surface and at depth, as well as to detect and quantify oceanographic anomalies during 2010 and link them to the penguins behavioural and reproductive anomalies.

To detect and quantify such oceanographic patterns and anomalies in the penguins' foraging area during 2010, we used frontal positions and SST values in the area to the south-east of Kerguelen.

a - Indices of frontal positions in the area to the south-east of Kerguelen

Surface positions of oceanographic features, particularly of the PF, can be determined from different parameters such as SST (Orsi et al. 1995; Park et al. 1998b; Moore et al. 1999b) or SSH (Sokolov & Rintoul 2009; Venables et al. 2012).

The PF surface signatures were defined as: (1) 4-4.2°C from SST, corresponding to the southern boundary of the 4-5°C PF signature (Park et al. 1998); and (2) -58.6 to -59.6 dyn.cm from SSH, corresponding to the mean PF summer signature ± 0.5 dyn.cm

following Venables et al. (2012). As there are contrasting definitions of the FTC surface signature in the literature (Park et al. 1998; van Wijk et al. 2010; Park & Vivier 2011), SST and SSH signatures for the FTC were determined as the 11-year means of SST and SSH in the Fawn Trough canyon from 1998-2009, thus characterizing the surface expression of the flow through the Fawn Trough without making pre-assumptions about frontal assignments.

b -Mapping of spatial and temporal variability in frontal positions

Mapping of SST and SSH surface signatures of the PF and FTC as defined above allowed visualization of the frontal positions in the area to the south-east of Kerguelen. To investigate long-term oceanographic patterns during the study months of January and February we mapped the 11-year monthly means for January and February with the interannual monthly variability envelope of the PF and the FTC. To explore oceanographic conditions during a particular year and determine differences to the long-term situation, we computed monthly mean and weekly variability envelope contours of the SST and SSH signatures during January and February in a particular year and overlaid these onto the 11-year mean and variability envelope. To investigate small-scale oceanographic variability we also included the daily SST variability envelope (not possible for SSH due to lower temporal data resolution).

c -Investigation of long-term oceanographic patterns in the foraging area of king penguins

To investigate long-term variability in oceanographic patterns in the foraging area of king penguins, we used frontal positions determined from Ostia SST data, and SST at defined locations in the area to the south-east of Kerguelen. Indices of frontal positions in the area to the south-east of Kerguelen were determined from SST signatures, as SST provided the best surface evidence for shifts in the FTC from visual inspections of the SST and SSH signature maps (see Figures 5.8 and 5.9). Frontal positions based on spatial patterns of SST signatures were determined in the area between 55-60°S, 80-82°E, where the FTC reaches

its northernmost position to the south-east of the Kerguelen Plateau and approaches the PF above the Chun Spur. In this context we assessed the following three indices: i) The PF position was defined as the southernmost position of the 4°C contour, corresponding to the southern boundary of the 4-5°C PF signature (Park et al. 1998), and ii) the FTC position as the northernmost position of the 1.5°C contour within the defined area (chosen from visual inspection of SST contour maps at the FTC, see above in part b). iii) SST was determined in a restricted area to the north of the Chun Spur (52-53°S, 80-82°E), representing the area of cold FTC flow across the Chun Spur into the area to the south-east of Kerguelen (Roquet et al. 2010). The evolution of SST in this area in relation to the PF and FTC positions allowed assessment of the impact of these features on oceanography in proximity of the Chun Spur, as well as evaluation of whether SST in this area may be a representative measure of the frontal positions, particularly the PF position, in the area to the south-east of Kerguelen. Mean and percentiles at the 5% and 95% level were determined for the timeseries of PF and FTC positions as well as SST at the Chun Spur for February for 1998 to 2011 to identify derivations from the mean conditions, and quantify the anomaly which occurred in February 2010. We smoothed the time series using a 11-day running mean window in order to focus on the most persistent signals with potentially stronger impacts on oceanographic conditions in the foraging area of king penguins.

5.4 Results

5.4.1 Trip parameters, body mass gain, arrival dates at the colony for egg laying, egg and chick abandonment

During the 2009/10 breeding season, the phenology was delayed, with most breeders laying 1.5 months later than in normal years (pers. obs.). Foraging trips in 2010 were longer than in any other year (Fig. 5.1, Table 5.1). Due to the long foraging trip durations there were high rates of egg and chick abandonment before the partner's return to the colony (94% abandon in both study and control birds). Mean duration until abandonment was 27.2 days after the partner's departures to sea. The mean body mass of the partner on shore at egg/chick abandonment was 9.1 kg (Table 5.1).

	Study birds	Control birds	Total
Number of birds equipped	17	30	47
Trip duration (days)	39.02 ±2.56 (n=11)	32.61±0.53 (n=27)	34.81±0.86 (n=38)
Body mass at trip start (kg)	9.88±0.15	9.97±0.15	9.94±0.11
Body mass gain (kg)	3.96 ±0.21 (n=9)	4.94±0.2 (n=27)	4.69±0.17 (n=36)
Daily body mass gain (kg)	0.11±0.01 (n=9)	0.15±0.01 (n=27)	0.14±0.01 (n=36)
% egg/chick abandon	100%	90%	94% (3/47 successful)
Days until abandon	25.5 ±0.87 (n= 10)	28.25±1.31 (n=16)	27.19±0.9 (n=26)
Body mass of partner at abandon (kg)	9.16±0.21 (n=5)	9.07±0.15 (n=10)	9.1±0.12 (n=15)

Table 5.1: Trip duration, body mass gain and egg/chick abandon times for study and control birds in 2010. Additional n-values are given where the number of birds used for calculation was different from the number of birds equipped given in the table.

5.4.2 Surface behaviour at sea

Foraging trips in February 2010 extended to greater distances from the colony than in any other year, extending further to the south-east of Kerguelen (Fig. 5.1). Compared to other years, king penguins foraged in deeper waters and encountered higher geostrophic velocities (Fig. 5.2 a,b). Foraging locations had values for SSH which were shifted, away from the PF towards more southerly SSH signatures, with values more characteristic of the

southern PF to the SACCF (Fig. 5.2c). The exploration of more offshore oceanographic features of elevated geostrophic currents at greater distances from the colony is illustrated by the example track from one penguin in Annex A.

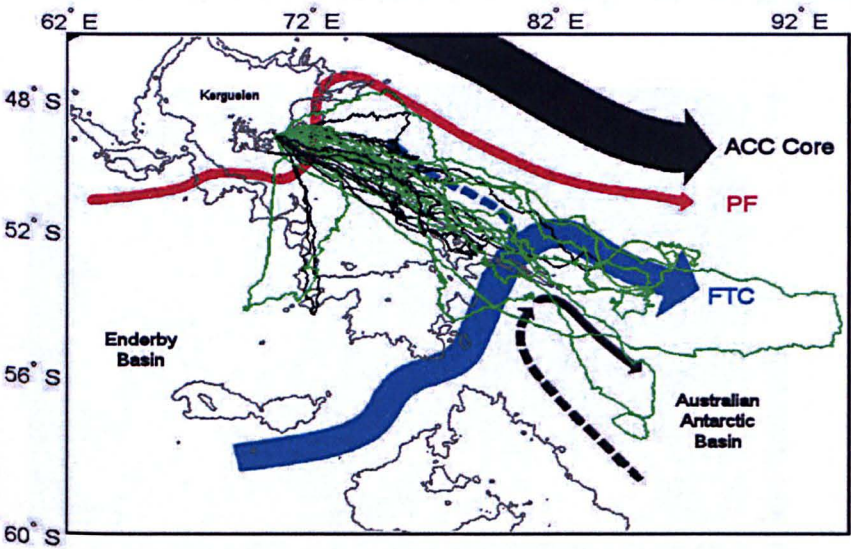


Figure 5.1: Foraging trips of incubating king penguins in 2010 (green) and during other years (black) in relation to local oceanography at Kerguelen. Coloured arrows show the main oceanographic features in the Kerguelen area (from Park et al. 2008b). ACC = Antarctic Circumpolar Current; PF = Polar Front; FTC = Fawn Trough Current. Grey lines show bathymetry contours at 0, 1000 and 2000m depth.

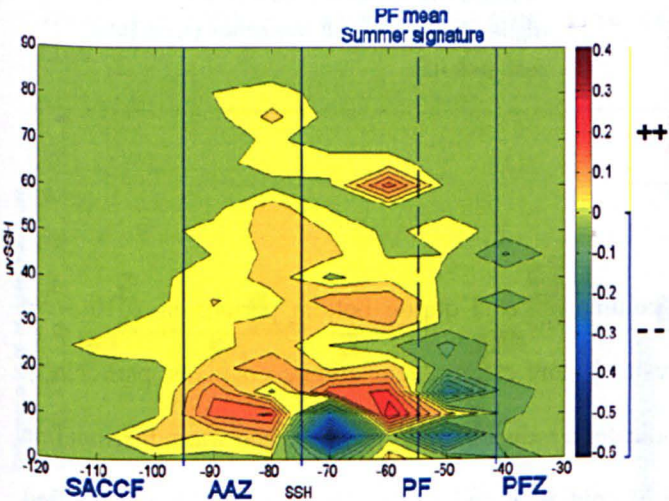


Figure 5.2: Changes in foraging habitat exploration in 2010: differences in SSH and geostrophic velocities explored at foraging locations between 2010 and other years. Values from 0-1 (yellow-red shadings) correspond to enhanced exploration in 2010, values from -1-0 (blue shadings) to reduced exploration in 2010. A value of 0 (light green shading) corresponds to no differences. Details of the method may be found in Material & Methods. Blue limitations show the different ACC frontal zones based on SSH signatures from Venables et al. (2012). PFZ – Polar Frontal Zone; PF – Polar Front; AAZ – Antarctic Zone; SACCF – Southern ACC Front.

5.4.3 Diving behaviour and water masses explored

The number of wiggles per dive and the dive efficiency were significantly reduced in 2010 compared with other years (Fig. 5.3a-c). Physiological dive effort, represented by the product of dive rate and bottom start depth, were significantly higher in 2010 (Fig. 5.3d).

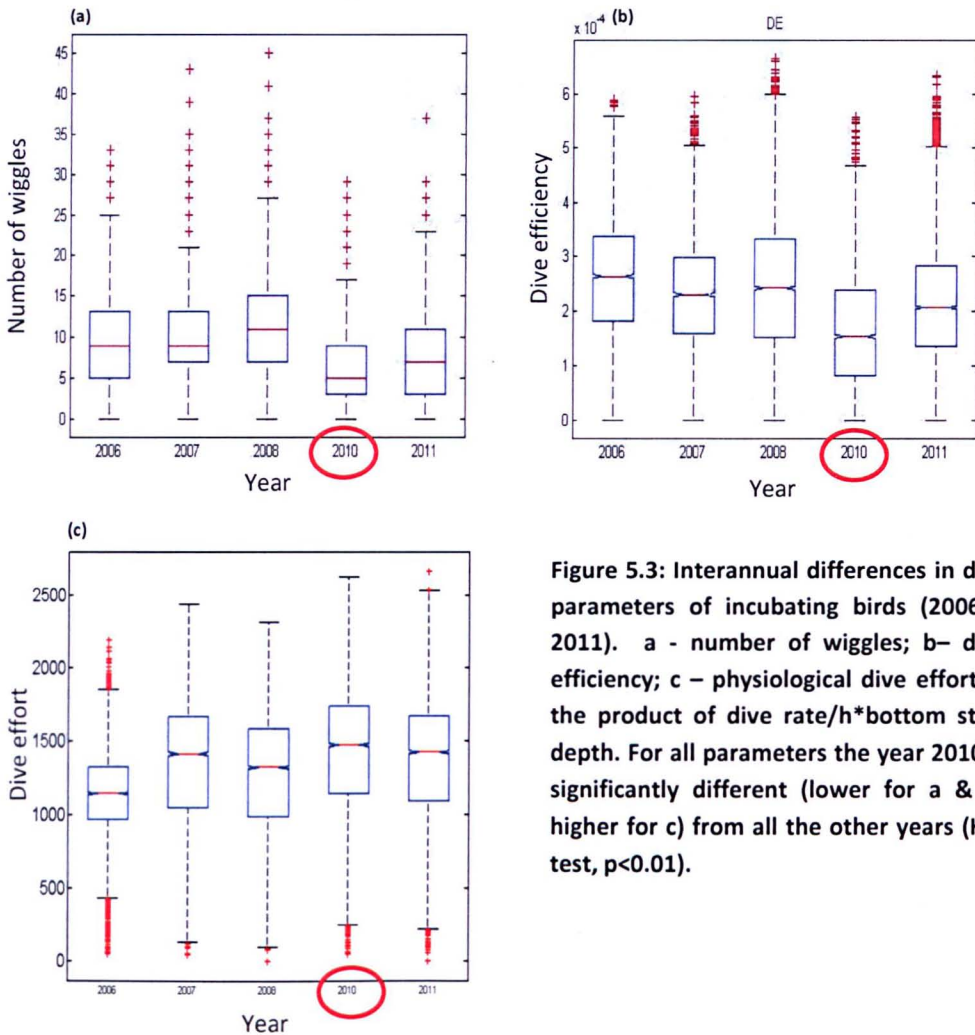


Figure 5.3: Interannual differences in dive parameters of incubating birds (2006 – 2011). a - number of wiggles; b – dive efficiency; c – physiological dive effort (= the product of dive rate/h*bottom start depth. For all parameters the year 2010 is significantly different (lower for a & b; higher for c) from all the other years (KW test, $p < 0.01$).

Thermal properties in the water column targeted during bottom periods in 2010 were shifted towards colder temperatures and more extreme temperature gradients, particularly towards positive gradients. This indicates a reduced use of the SML and warm thermocline waters, and enhanced exploration of cold WW and CDW. The use of WW was shifted towards colder temperatures (Fig. 5.4). Shifts in water mass exploration during bottom

periods showed differences depending on specific SST zones (Fig. 5.5). In the PFZ and PF (SST >4°C), the SML and the thermocline (TH) use was decreased and WW use increased. In areas of SST <3°C, CDW and cold WW exploration replaced use of the TH and SML in SST >3°C, and WW in SST <2°C.

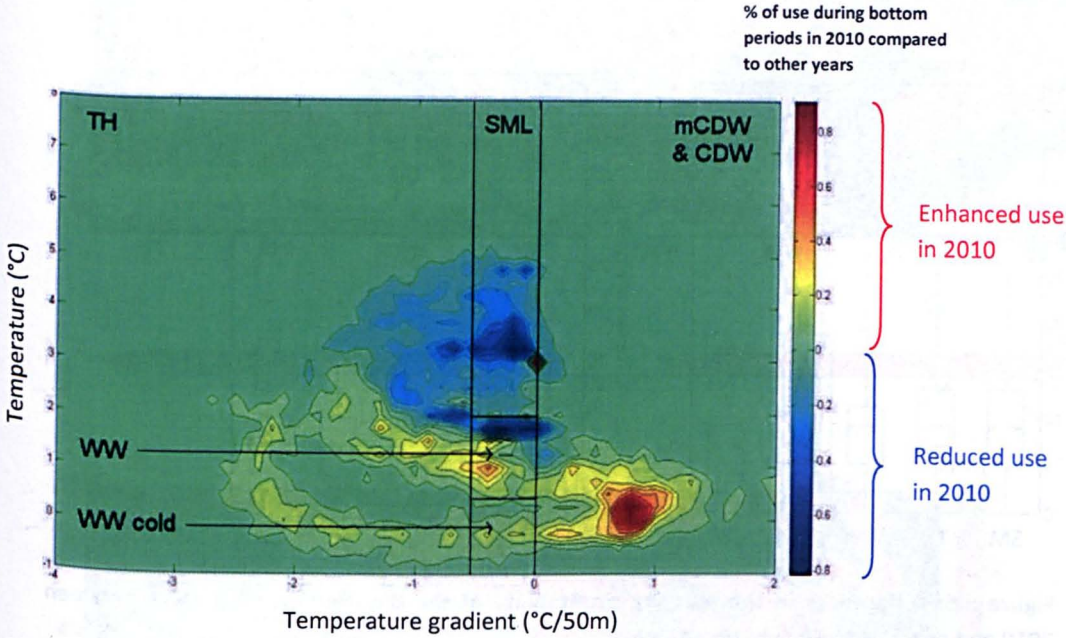


Figure 5.4: Differences in thermal properties of the water column explored during bottom periods between 2010 and other years. Values from 0-1 (yellow-red shadings) correspond to enhanced exploration in 2010, values from -1-0 (blue shadings) to reduced exploration in 2010. A value of 0 (green shading) corresponds to no differences. Details of the method may be found in Material & Methods. SML – Surface Mixed Layer; TH – Thermocline; WW – Winter Water; WWc – cold WW (<0.5°C); CDW – Circumpolar Deep Water; mCDW – modified CDW.

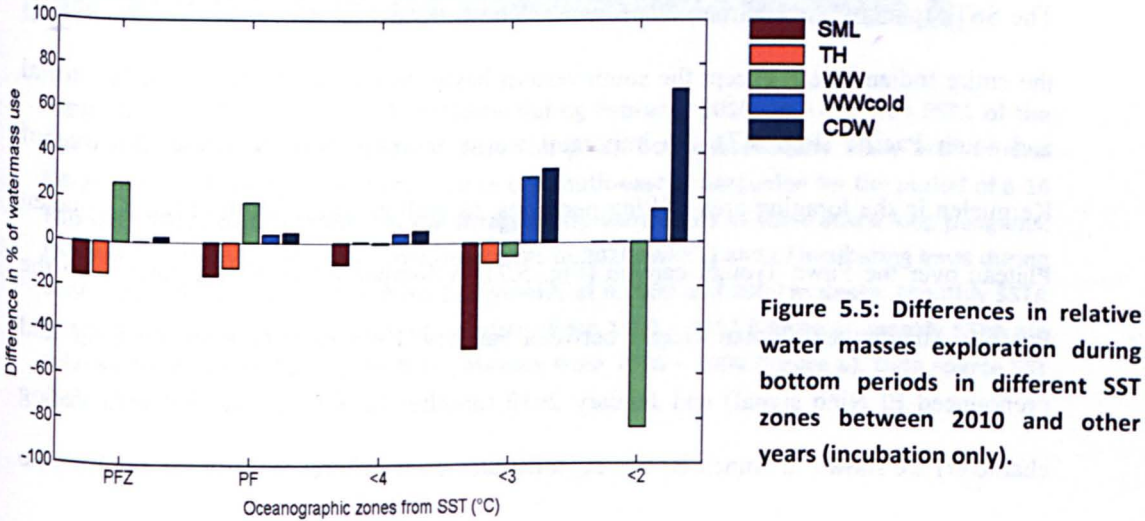


Figure 5.5: Differences in relative water masses exploration during bottom periods in different SST zones between 2010 and other years (incubation only).

Foraging profitability was significantly reduced in 2010 in the SML, TH, WW and cold WW, in terms of the number of wiggles per dive carried out in a specific water mass as well as the dive efficiency. There were no significant differences for dives directed into CDW (Fig. 5.6).

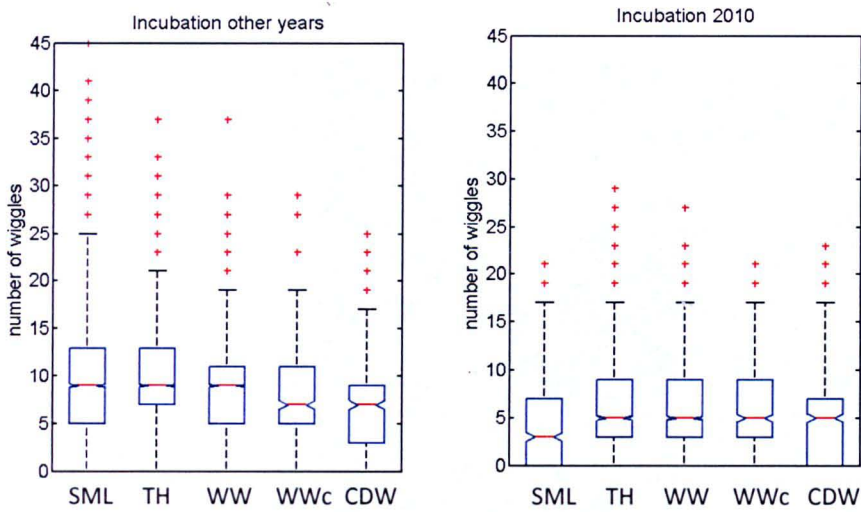


Figure 5.6: Differences in the foraging profitability of the different water masses between 2010 and other years (incubation only).

5.4.4 Environmental conditions during February 2010

5.4.4.1 SST

The SSTA patterns for February 2010 were characterized by warm anomalies throughout the entire Indian Ocean except the southwestern basin, as well as in the central equatorial and south Pacific (Fig. 5.7). An important warm anomaly was located to the east of Kerguelen in the foraging area of king penguins, as well as to the south of the Kerguelen Plateau over the Fawn Trough canyon (Fig. 5.7). A comparison of SSTA patterns in the Pacific, Atlantic and Indian Ocean between January 1998 (a year with a strong and pronounced El Niño signal) and January 2010 (another El Niño signal, but of differing character) are shown in Annex B; this demonstrates clear differences between the El Niño

SST patterns during both years, with the centre of the warm anomaly situated in the eastern Pacific during 1998, and in the central Pacific during 2010.

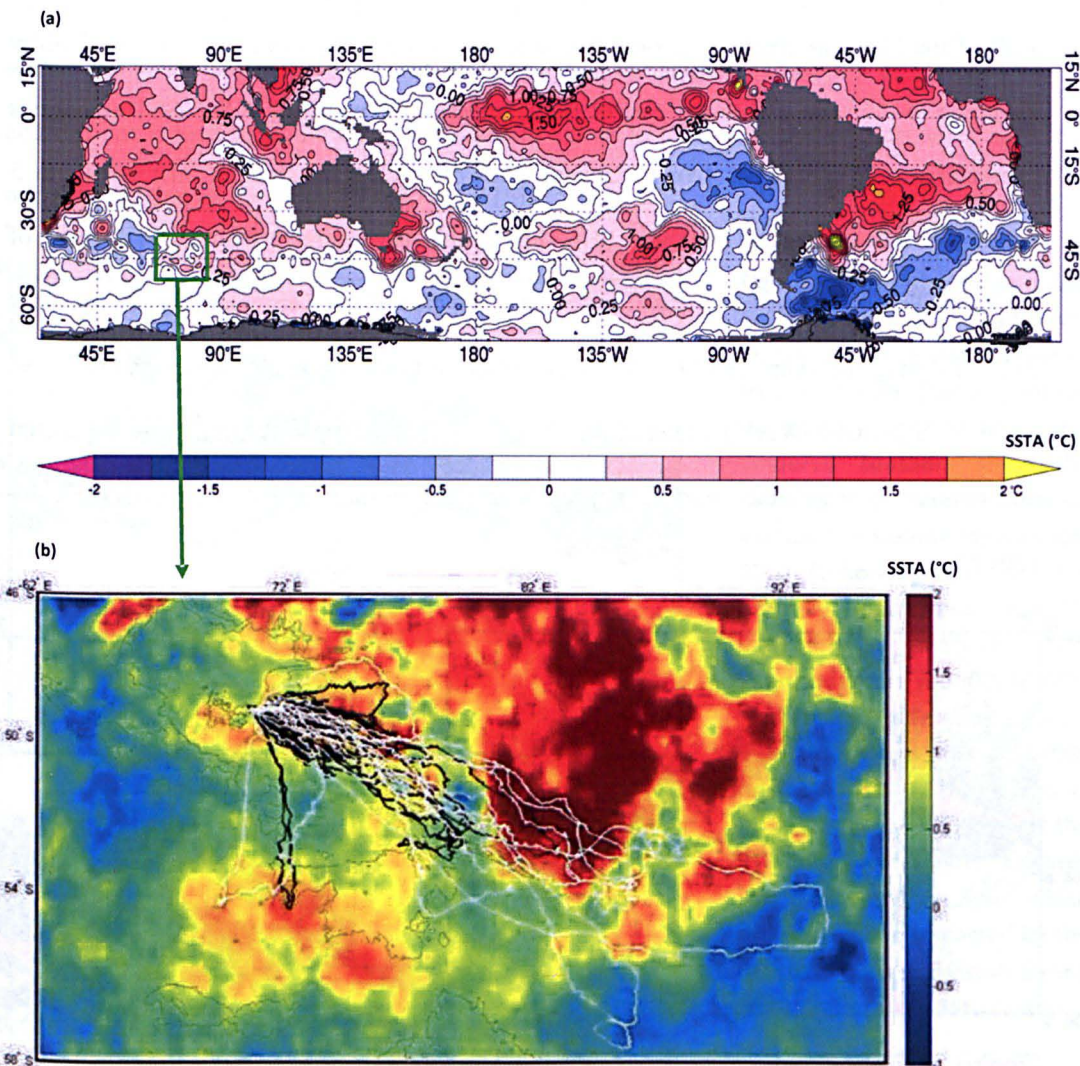


Figure 5.7: SST Anomalies (SSTA) patterns during February 2010. a – Monthly SSTA of the Southern Hemisphere for February 2010. The green box indicates the study area around Kerguelen. b – Weekly SSTA in the area to the south-east of Kerguelen for the period of 8-14 February 2010, corresponding to the foraging trip start dates of the tracked king penguins. Overlaid are the king penguins’ foraging tracks of 2010 (white) and of incubating birds during other years (black). Grey lines show bathymetry at 0,1000 and 2000 m depth. Monthly SSTA are relative to the mean SST during February from 1950 – 2011 (Figure a); weekly SSTA are relative to the mean SST during 8-14 February from 1998 – 2009 (Figure b). Data source SST data: Met Office.

5.4.4.2 Frontal positions from SSH and SST signatures

The monthly mean and daily SST signatures during February 2010 showed a southward shift of the PF away from the geographic position occupied by the interannual variability envelope to the west and to the east of the Kerguelen Plateau (Fig. 5.8a). SST signatures characteristic of the Fawn Trough Current showed a clear southward shift by up to 5 degrees of latitude during February 2010 (Fig. 5.8b). The characteristic SST signature of the Fawn Trough Current over the Chun Spur to the east of the Kerguelen Plateau reaching to 53°S during the years 1998 to 2009 was shifted to the south and only reached latitudes of 56-58°S in 2010. Weekly maps of the PF and FTC SST signatures underline the abrupt and temporally restricted nature of patterns occurring during February 2010 (figures not shown).

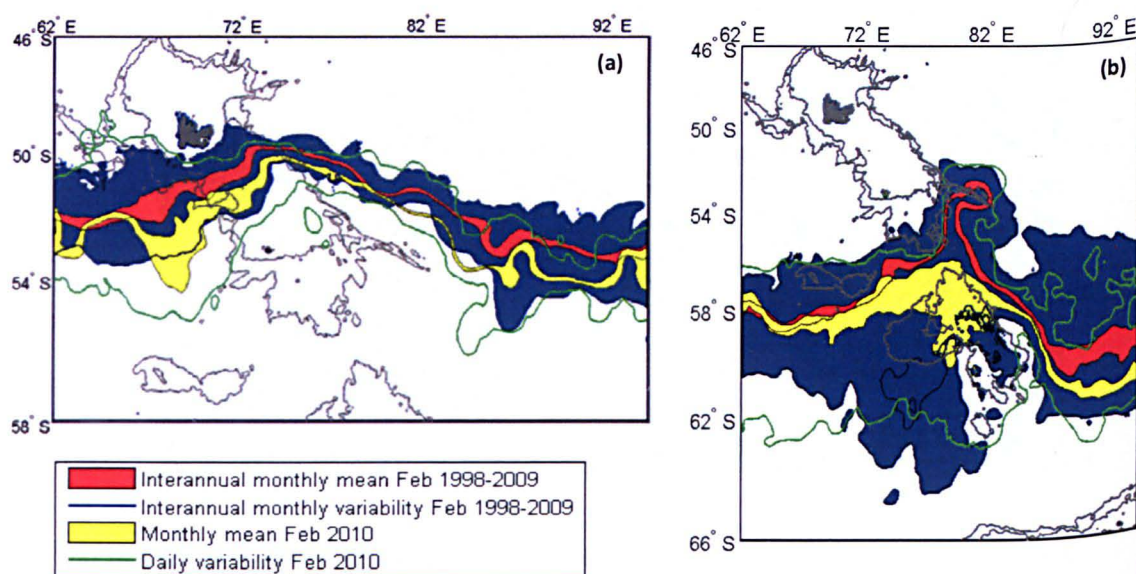


Figure 5.8: Monthly maps of Sea Surface Temperature (SST) isotherms during February corresponding to a - the PF (4-4.2°C) and b - the FTC (1.4-1.6°C). Coloured contours show the monthly mean and the daily variability envelope for February 2010 (yellow, green) and the monthly mean and monthly variability envelope for February of the years 1998-2009 (red, blue). Grey lines indicate bathymetry at 0, 1000 and 2000 m depth. Data source: Met Office.

The SSH signatures during February 2010 showed a southward shift of the PF to the west of the Kerguelen Plateau, and southward extending meanders to the east of the plateau near the Chun Spur (Fig. 5.9a). The Fawn Trough Current SSH signatures did not show shifts within the Fawn Trough canyon, but was shifted to the south downstream of the canyon and did not extend over the Chun Spur into the area to the south-east of Kerguelen as it normally did during the years 1998 to 2009 (Fig. 5.9b).

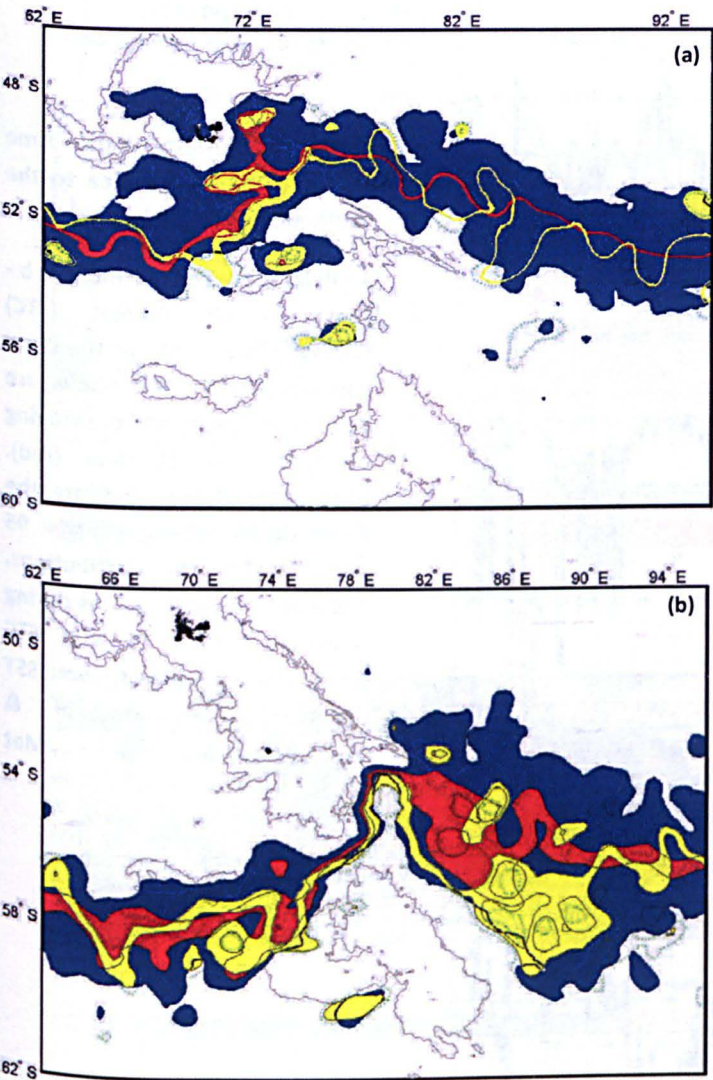


Figure 5.9: Monthly maps of Sea Surface Height (SSH) signatures during February corresponding to a - the PF (mean summer signature) and b-the FTC. Coloured contours show the monthly mean and the weekly variability envelope for February 2010 (yellow, green) and the monthly mean and monthly variability envelope for February of the years 1998-2009 (red, blue). Grey lines indicate bathymetry at 0, 1000 and 2000 m depth. The purple arrows in (a) indicate the direction of the FTC northward flow towards and over the Chun Spur, which may have been impacted by the PF southward extension during 2010. Data source SSH: Aviso.

Due to the evident southward shift of the PF, the distances between the PF and the Chun Spur were the smallest since 1998 based on both SST and SSH signatures. The southward positions of the PF and the FTC as well as the SST at the Chun Spur exceeded the 95th percentiles of all years since 1998, with extreme southward frontal positions and high SST at the Chun Spur (Fig. 5.10):

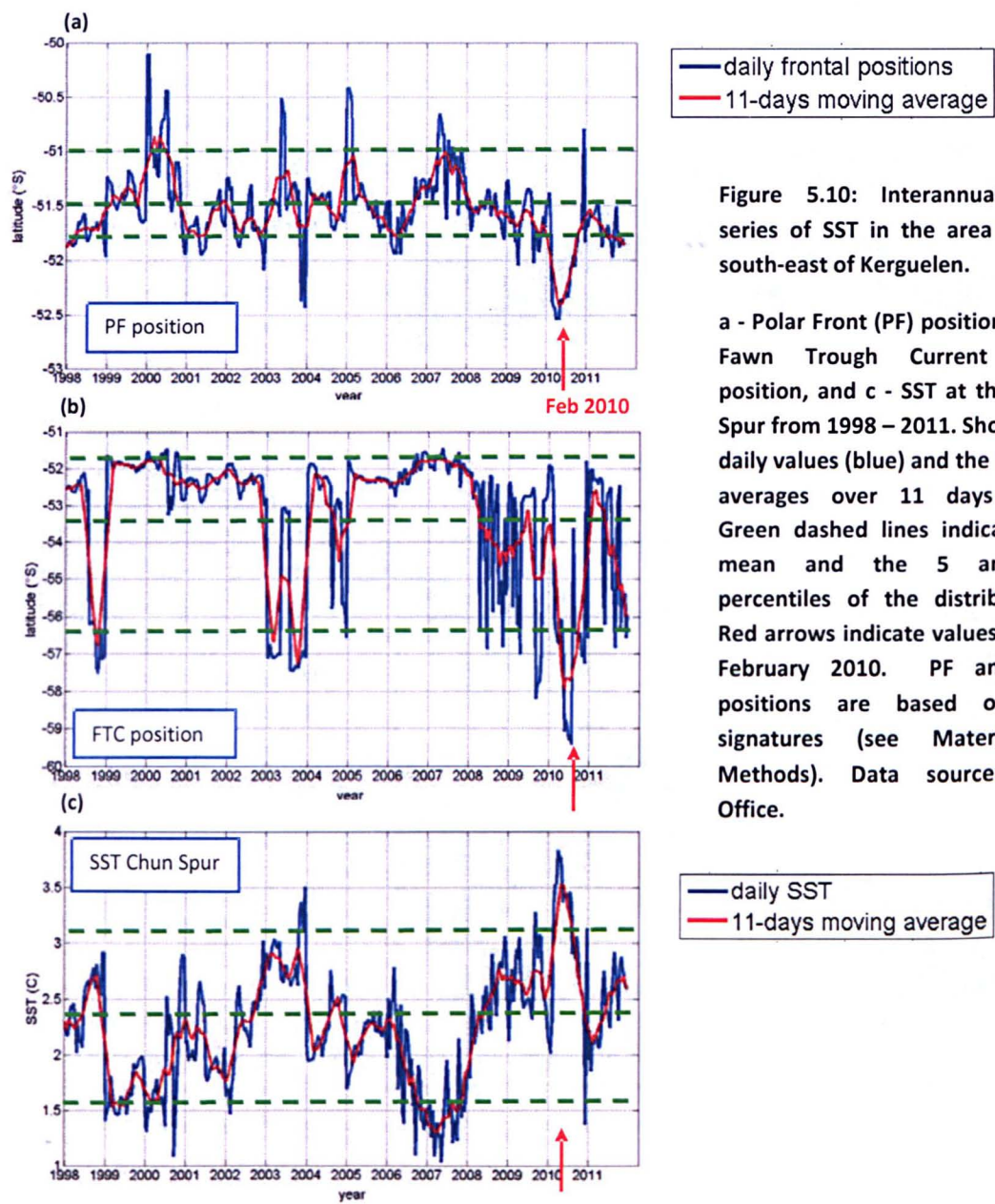


Figure 5.10: Interannual time series of SST in the area to the south-east of Kerguelen.

a - Polar Front (PF) position, b - Fawn Trough Current (FTC) position, and c - SST at the Chun Spur from 1998 – 2011. Shown are daily values (blue) and the moving averages over 11 days (red). Green dashed lines indicate the mean and the 5 and 95 percentiles of the distributions. Red arrows indicate values during February 2010. PF and FTC positions are based on SST signatures (see Material & Methods). Data source: Met Office.

5.4.4.3 Atmospheric processes

In February 2010, Mean Sea Level Pressure (MSLP) patterns around Kerguelen were reversed to the normal situation, with an extended high-pressure system to the south and a more local but pronounced low-pressure system to the north of the island (Fig. 5.11a). Wind anomaly maps showed a strong anomaly in the south Indian Ocean, indicating a cyclone over the Kerguelen area (Fig. 5.11b). Detailed maps showing the evolution of the MSLP patterns during late January and early February 2010 may be found in Annex C.

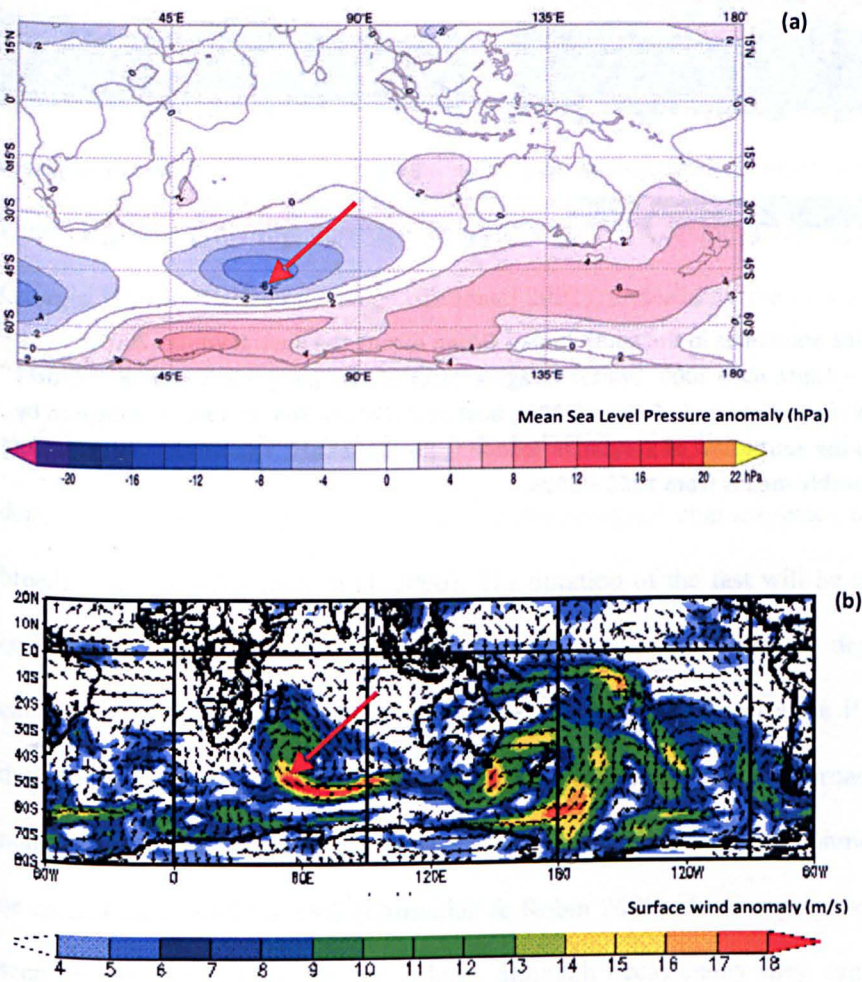


Figure 5.11: Mean Sea Level Pressure (MSLP) and wind anomalies in the south Indian Ocean during February 2010. a – monthly composite of MSLP anomalies; b – 1-day snapshot of wind anomalies for the 4 February 2010, showing the presence of a pronounced storm in the Kerguelen area. in (b) contours indicate the intensity, arrows the direction of the anomaly. The red arrows indicate the location of Kerguelen. Data: Met Office; NOAA NCEP.

5.4.4.4 Sea-ice patterns during austral winter 2009

Sea ice concentration showed positive anomalies in the area between 70-90°E, and negative anomalies between 30-70°E during August and September 2009 (Fig. 5.12 a,b).

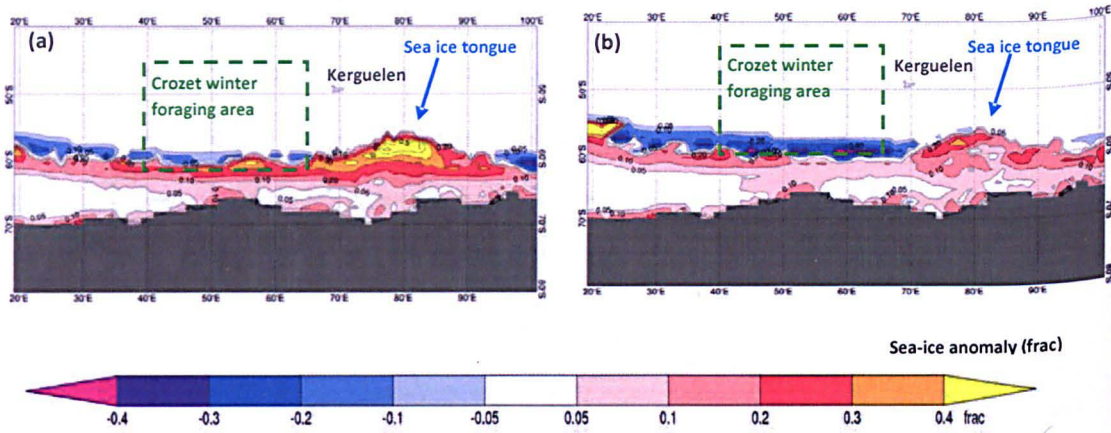


Figure 5.12: Sea-ice anomalies in the south Indian Ocean during the austral winter 2009. a – August 2009; b – September 2009. Winter foraging areas of king penguins breeding at Crozet (green dotted box) from Charrassin & Bost (2001), Bost et al. (2004). Sea-ice tongue indicated by the blue arrow to the south-east of Kerguelen following Rintoul et al. (2008). Sea-ice anomalies are relative to monthly means from 1950 – 2009.

5.5 Discussion

The breeding season of 2009/10 was characterized by anomalies in both behaviour and reproductive success for king penguins breeding at Kerguelen. The observed anomalies in foraging trip duration and egg/chick abandonment rate were the most extreme observed since the beginning of the Kerguelen long-term monitoring programme in 1998. King penguin foraging trips were to locations that were 75% more distant and further afield from the colony than on average; they also lasted up to 52% longer than in other years. Furthermore, and of very considerable ecological importance, the breeding failure rate was 94% and exceeded all previous records of such anomalous events at Kerguelen. Moreover, in 2010, the failure for king penguins at Kerguelen exceeded all other similar events for kings recorded in the literature (Crozet 1993/94: 47%, Gauthier-Clerc et al. 2001; South Georgia 1994: 60%, Olsson & van der Jeugd 2002), underlining the extreme nature of the 2010 event.

King penguins can fast for over a month when incubating, with the maximum duration dependent upon sex, experience, body size/physiological characteristics and time of the breeding season (Groscolas et al. 2000). The duration of the fast will be allied to critical body mass (cMb), which is reached when fat stores are critically depleted and the catabolism of the animal shifts from a stage of protein sparing (phase II) to a stage of dramatically increased protein catabolism (phase III). As birds approach this critical nutritional state, their metabolism triggers their return to sea and abandonment of their egg or chick before reaching cMb (Groscolas & Robin 2001). As it approaches birds can be seen abandoning their egg in the colony, although occasionally they can sometimes be observed moving towards the edge of the colony and even down to the beach, where they eventually abandon their egg and leave to go to sea (P.N. Trathan pers. obs.). In our study, birds abandoned their egg or chick between 22 and 43 days (27.2 ± 0.9 days, mean \pm SE),

with body masses ranging between 8.0 and 9.8 kg (9.1 ± 0.2 kg). These values are approaching the critical body mass values for when birds move from phase II to phase III (8.78 kg, Groscolas et al. 2000; 9.6-10.0 kg, Groscolas et al. 2008), or during moult (9.62 ± 0.17 kg, Cherel et al. 1994; 9.62 ± 0.33 kg, Halsey et al. 2008). Validation of critical body mass against predicted values from Halsey et al. (2008) was not possible, as morphological characteristics of incubating partners abandoning the egg during the extended foraging trips of our study birds were not recorded.

Extended foraging trips and high total body mass gain together with breeding abandonment may reflect trade-offs for long-lived birds, with the trade-off favouring adult survival to that of offspring survival (Stearns 1992; Gauthier-Clerc et al. 2002; Groscolas et al. 2008). Such a situation confirms model predictions for king penguin parents, providing for their own needs in case of low food availability (Cresswell et al. 2012). Such decisions may also reflect late arrival on land prior to egg-laying, possibly as birds build up their safety margins in terms of body reserves; this may be particularly important if body condition is low after there have been poor winter/spring foraging conditions. Late arrival may result in higher risks of breeding failure if there is insufficient chick rearing time and inadequate prey resources later in the season (Gauthier-Clerc et al. 2002).

The breeding and foraging behaviour of king penguins, particularly their foraging trip duration, can be used as indicators of variability in prey availability (Gauthier-Clerc et al. 2002), and in the marine ecosystem in general (Le Maho et al. 1993). This suggests that important changes in marine resources occurred in the area to the south-east of Kerguelen during the austral summer of 2010.

5.5.1 Oceanographic and behavioural anomalies during the pre-breeding and breeding season of 2009/2010

King penguins clearly experienced anomalous conditions resulting in unusual behaviour during the pre-breeding season in 2009; this was manifest as delayed arrival on land at the start of the breeding season (2 months delay). Later, after breeding commenced, we observed changes in foraging behaviour during February 2010.

Late 2009 and early 2010 were characterized by significant oceanographic anomalies in the Indian Ocean, with a basin-wide warming from July to October 2009 (Arndt et al. 2010), and high SST and southward shifts of the PF and FTC in the area around Kerguelen during February 2010. King penguins are characteristically highly oceanic foragers; the behavioural and reproductive anomalies observed for king penguins during 2009/10 are therefore highly likely to be related to the anomalous oceanographic conditions observed in the Indian Ocean.

The PF shifting out of the 11-years SST and SSH variability envelopes suggests that the anomaly occurring in 2010 was the most pronounced since 1998, with drastic impacts on king penguins behaviour and breeding success. It is therefore plausible that extreme behavioural and reproductive patterns make 2010 a unique event, and at least partly related to the southward shifts of the PF. This may have been related to changes in oceanographic processes and water column properties in the Chun Spur area, particularly in king penguin foraging habitat in the upper ocean.

5.5.1.1 Pre-breeding period, austral winter and spring 2009

The significantly delayed arrival prior to egg laying was highly likely to be caused by the prevailing oceanographic conditions during the period prior to the penguins' arrival on

land; most probably during the winter or during the post-moulting foraging trips in 2009. Currently, there is no documented information about the winter or post-moult distributions of king penguins breeding at Kerguelen, making it difficult to draw definitive conclusions about factors impacting the birds behaviour prior to breeding. However, king penguins at Kerguelen may show similar behaviour to those breeding at Heard Island and Crozet, which explore areas related to the ice-edge south of their breeding colony during winter, and areas close to the PF during post-moulting in spring (Moore et al. 1999a; Charrassin & Bost 2001; Bost et al. 2004). The sea-ice anomalies to the south of Kerguelen during August/September 2009 may therefore have impacted king penguins during their winter foraging trips. As king penguins breeding at Crozet did not show behavioural anomalies, sea-ice anomalies that may have impacted king penguins breeding at Kerguelen are likely to be situated in areas different from those explored by Crozet birds during winter (40-67°E, Charrassin & Bost 2001; Bost et al. 2004). The pronounced positive sea-ice anomaly to the south-east of the Kerguelen Plateau (~70-90°E, see Fig. 5.12) is therefore the most likely ice-related anomaly that may have impacted the winter foraging of king penguins from Kerguelen. In the area near 85°E, a pronounced sea-ice tongue has been reported to occur during some winters (Rintoul et al. 2008). The sea-ice tongue as well as a related northward current in this area have been suggested to play an important role for the high biomass in this area, ranging from primary production (Tynan 1997; Nicol et al. 2000; Rintoul et al. 2008) to upper trophic levels such as cetaceans (Tynan 1997; Tynan 1998; Nicol et al. 2000). It is therefore possible that this area also plays an important role for foraging king penguins during winter. Sea-ice related anomalies in this area may therefore have impacted the penguins' winter foraging success. However, due to the lack of available information concerning winter and spring movements of king penguins at Kerguelen these hypotheses remain untested.

In the austral spring, the eastern Indian Ocean exhibited significant basin-wide warming from October 2009, which may have impacted king penguin prey, foraging behaviour and foraging success during their post-moulting trips. If birds had been unable to recover condition from moulting (Gauthier-Clerc et al. 2002) and had lower than normal reserves prior to commencing breeding, penguins may have been forced to prolong their post-moulting trips by staying longer at-sea, resulting in their delayed arrival on land for breeding. Body mass at the start of their incubation foraging trips suggests that there were no significant differences in the physiological condition of penguins in 2010 compared with other years. Low body mass at arrival has been reported to lead to early egg abandonment for king penguins breeding at Crozet (Le Maho et al. 1993; Gauthier-Clerc et al. 2001). As there was no obvious statistically significant reduction in initial body mass at Kerguelen during 2010, it suggests that birds may have been able to compensate for winter conditions by their late arrival to breed. This further suggests that changes in foraging behaviour observed during incubation and the subsequent poor reproductive success may have been mainly related to the feeding conditions encountered during breeding, and not caused by the winter/spring conditions. Late breeding is known to decrease chick survival due to decreased marine resources later in the season (Gauthier-Clerc 2002). A delayed start to breeding may thus decrease the chances of breeding success and may indicate that birds decided to favour their own body reserves instead of offspring survival, possibly in a similar manner to that of king penguins at South Georgia in 1994 (Olsson & van der Jeugd 2002). Of course the continued warm conditions during incubation may have meant that the poor feeding conditions continued, and though birds were able to compensate for the poor winter conditions, they could not compensate for the prolonged anomalous conditions and breeding failure was inevitable.

5.5.1.2 Breeding period, February 2010

King penguin foraging trips during February 2010 extended beyond the foraging range of other years with birds travelling further to the south-east. A number of significantly decreased dive parameters also suggest that birds may have experienced less favourable foraging in 2010 compared with other years. Such decreased foraging performance together with increased physiological effort in terms of at-sea time and dive effort is highly likely to reflect reduced prey availability in the usual foraging area (Piatt & Sydeman 2007, suggesting that oceanography and associated prey resources may have been altered in a way that king penguins were not able to compensate for by foraging successfully.

5.5.1.2.a Oceanographic changes: ocean warming and shifts in key oceanographic features in the foraging area of king penguins

February 2010 was characterized by pronounced warm SSTA to the east and south-east of the Kerguelen Plateau as well as in the FT canyon. As these areas are thought to be key locations for king penguin foraging (see Chapter 4), the observed changes in behaviour and reproductive anomalies may have been related to the oceanographic conditions in these locations. Significant southward shifts in PF and FTC surface signatures reflect the warm SSTA, and indicate changes in key oceanographic features in the foraging area of king penguins to the south and south-east of Kerguelen. Shifts were most obvious from SST isotherms, suggesting that in-situ warming and anomalies in upper-ocean processes played an important role. Vertical heat transfer from the ocean surface through turbulent mixing may alter thermal conditions in the upper water column in such a way as to cause changes in the distribution of myctophids, which are known to be highly sensitive to thermal conditions in their environment (Hulley 1981; Kozlov et al. 1991). As king penguins explore relatively shallow water masses (0-350m, Charrassin et al. 2001), such surface warming may impact oceanographic structures and associated prey resources. The effects

of such surface warming and changes in subsurface oceanography may be further amplified by changes in circulation patterns. In addition to shifts in SST isotherms, the PF SSH signatures showed extended southward meanders away from the southern variability envelope to the south-east of the Kerguelen Plateau, indicating deep-reaching circulation changes in the area. The PF is associated with important changes in physical properties of the water column, such as the northernmost extent of WW $<2^{\circ}\text{C}$ at 200 m depth (Orsi et al. 1995; Belkin & Gordon 1996; Park et al. 1998b). Changes in the path of the PF flow, indicated by SSH signatures, therefore reflect shifts in water column properties and oceanographic processes at depth, which may in turn impact water mass distribution in adjacent areas. The PF approached the Chun Spur to its nearest distance since 1998, based on both SST and SSH signatures, implying important oceanographic changes in the Chun Spur area, potentially amplifying the effects of in-situ warming.

Circulation patterns around the Kerguelen Plateau are complex and difficult to evaluate from surface characteristics. The absence of combined GPS/Argos - TDR datasets for 2010 makes it impossible to draw detailed conclusions about spatial patterns within the water column structure from the available TDR temperature data. Hypotheses about the spatial processes at depth must therefore remain speculative. Nevertheless, oceanographic patterns observed at the surface from remote sensing and from TDR temperature profiles during February 2010 support our suggestions regarding oceanographic patterns.

5.5.1.2.b Behavioural changes

Foraging area shifts from the Kerguelen Plateau to offshore areas/oceanic processes

The disruption of oceanographic conditions at the PF and in the Chun Spur area appeared to reduce foraging habitat suitability in the immediate proximity to the Kerguelen Plateau for king penguins. Foraging habitat shifts to greater depths, into waters with stronger geostrophic velocities and into waters with higher SSH variability suggest birds increased their exploration of dynamic large-and mesoscale features in offshore waters, such as ocean currents and eddies. These contrast with the more normally targeted bathymetric-related processes such as upwelling and the local channelling of subsurface flows associated with the Kerguelen Plateau (see Chapter 4). The SSH signatures of targeted waters also clearly show birds were exploring more southerly foraging areas in the AAZ and SACCF, indicating that there was a decrease in the profitability of the PF for foraging. Such a decrease in foraging habitat suitability in the Kerguelen Plateau area may have significant impacts on marine predators. It may result in longer travel times at sea and decreased overall foraging trip efficiency due to the greater distances of foraging areas from the colony, and to the higher dynamics and therefore potentially lower stability and predictability of oceanographic features explored. A decrease in foraging habitat profitability at the Kerguelen Plateau, and a shift in foraging habitat to offshore areas, could also have negatively impacted other marine predators breeding or feeding at the Kerguelen Plateau during 2010.

Oceanographic change and vertical prey distribution

Diving behaviour indicates that the oceanographic changes in the area to the south-east of Kerguelen may have impacted the vertical distribution of king penguins' prey. Shifts in the temperature (T) and temperature gradient (gradT) targeted during dive bottom periods together with deeper bottom start depths suggests changes in how birds explored the water

column; this was also characterised by shifts of bottom periods from the SML, TH and WW, to water masses at greater depths such as the cold WW and CDW. The significantly reduced profitability of the SML, TH and WW (in terms of dive efficiency and prey capture attempts (number of wiggles)), indicates the important changes in prey resources in these water masses. Myctophids are thought to be sensitive to changes in their thermal environment (Collins et al. 2008; Collins et al. 2012). Heat transfer into the water column, by upper-ocean warming or changes in water mass distribution by circulation changes, may have changed the upper oceanographic habitat, e.g. the SML, TH and WW, to the south-east of Kerguelen in a way that changed the suitability for myctophids. As a consequence, king penguins may have been forced to explore alternative water masses at greater depth for their prey.

In the PFZ and PF, shifts from SML and TH to WW exploration suggest reduced prey availability in the upper ocean layer, presumably due to the immediate effects of heat transfer from the surface into the water column. The TH in particular, has been shown to be an important feature for foraging king penguins (Charrassin & Bost 2001; Scheffer et al. 2012) and other marine predators (Biuw et al. 2007; Dragon et al. 2012). Changes in the TH profitability for key foraging areas such as the PF (Bost et al. 2009), may have profound impacts on the foraging success and behaviour of marine predators, and may have led to the reduced foraging success of king penguins in February 2010. In areas to the south of the PF (SST $<3^{\circ}\text{C}$), shifts from WW to cold WW and CDW during bottom periods suggest reduced prey availability in WW. In areas of cold SST to the south of the PF, such as in the Chun Spur area and along the Kerguelen Plateau shelf break, WW is thought to be of particular importance for foraging king penguins, due to upwellings and the subsurface cold-water flow from the FTC (see Chapter 4). Upper oceanic warming in the Chun Spur area and the southward shift of the PF flow towards the Chun Spur in February 2010 may have led to anomalies in the subsurface cold-water flow and in the

upwelling processes, possibly altering prey resources associated with WW in these areas. However, due to the reduced return in combined TDR and GPS data, it is not possible to determine the extent to which changes in vertical foraging behaviour were related to alterations in the physical properties of the water column in the usual foraging areas, or to changes in foraging areas offshore.

Importance of CDW as an alternative water mass explored

Significantly increased exploration of the CDW during 2010 indicates the increased importance of this water mass for foraging king penguins. In contrast to the upper ocean water masses, such as the SML, TH and WW, the CDW showed no significant reduction in the proportional dive time used for bottom periods, and the least reduction in prey capture attempts. Similar proportions of prey capture attempts despite the greater depths of CDW and therefore the longer dive travel times associated with its exploration, suggest a higher profitability of prey resources in CDW compared with the upper ocean during 2010. CDW is found at greater depths than the upper ocean layers normally explored by foraging king penguins (SML, TH and WW, see Chapter 4). The CDW is usually less affected by any direct influences of atmosphere-ocean-seaice interactions, but is more affected by bathymetric steering (Roquet et al. 2009). It is therefore possible that due to this insensitivity to the atmosphere, the CDW may be a conservative and important water mass for foraging king penguins, when the upper ocean is affected by environmental forcing. Overall, the foraging profitability of the CDW may be small compared to the SML, TH and WW under normal conditions. However, the apparent stability of this water mass to environmental forcing may make it an important element for air-breathing diving predators in some seasons. At South Georgia, king penguins have been reported to explore the CDW close to the colony when under increased time and energy constraints during brooding. However, such CDW exploration only took place during short foraging trips, where

horizontal travel effort was small (Scheffer et al. 2012). Such exploration of the CDW may occur in response to insufficient prey resources at shallower depths in areas close to the colony, or to highly profitable prey in CDW. At Kerguelen, CDW exploration may occur in cases of insufficient prey resources in the upper water masses, as happened during February 2010. However, in contrast to South Georgia, it does not appear that the CDW provided sufficient foraging conditions at Kerguelen, as increased CDW exploration in 2010 was also associated with high breeding failure.

Diving to greater depths at higher costs: a behavioural response

Reductions in prey availability in the upper ocean appear to force king penguins to dive to greater depths. Prey pursuit at greater depths results in higher dive effort to reach prey, and a smaller proportion of dive time available for the actual prey pursuit phase. This may lead to reduced foraging efficiency in terms of CPUE during a dive, if the profitability of the prey, e.g. the patch density or the energetic value per unit, is not increased. If prey profitability stays constant, foraging effort may be increased to compensate the reduced foraging profitability (Charrassin et al. 1998). High dive effort in terms of dive rate * bottom start depth in 2010 indicates such increased physiological pressure on the penguins, where dive rate and depth may not have been equalized but both increased. Elephant seals from Marion Island have been reported to increase dive rates as a response to greater dive depths with less time in the bottom phase of the dives (McIntyre et al. 2011). However, king penguins increased both dive effort as well as surface travel effort and at-sea time, still leading to reduced foraging performance and breeding success. Significant disruptions in prey availability in the foraging area are likely to have caused such insufficient foraging conditions.

5.5.2 Connections to environmental variability at large and small scales

In-situ warming is potentially one of the main mechanisms for oceanographic anomalies in the Kerguelen area in February 2010, suggesting an important role of atmosphere-ocean interactions. Environmental variability at a variety of spatial and temporal scales probably played a role in generating the oceanographic conditions in the south Indian Ocean during 2009/10, and therewith the observed anomalies in king penguins behaviour. The occurrence of the strong oceanographic and behavioural anomalies only for king penguins at Kerguelen but not at Crozet (CA Bost, pers. comm.) suggests that behavioural anomalies of king penguins breeding at Kerguelen may have been caused by oceanographic conditions local to the sector of the Indian Ocean exclusively explored by king penguins breeding at Kerguelen and not by those breeding at Crozet. If such anomalies were related to patterns exceeding scales local to the eastern basin of the south Indian Ocean, there may have been mechanisms of transferring and potentially amplifying the signal to the Kerguelen area, but not to Crozet.

5.5.2.1 Connection to large-scale patterns: Pacific and Indian Ocean

Anomalies in king penguins foraging and reproductive success during 2009/10 were presumably related to oceanographic conditions in the Indian Ocean prior to and during breeding. In late 2009 and early 2010, the Indian Ocean was characterized by a significant basin-wide warming from remote El Niño impacts (Blunden et al. 2011), reaching a historical high with even higher SSTA than during the strong 1997/98 El Niño event (Blunden et al. 2011). The extreme nature and the spatial and temporal extent of the Indian Ocean warming in 2009/10, particularly in the eastern south Indian basin, suggests that this pattern may have impacted oceanographic conditions and therefore prey availability in king penguins' foraging areas during pre-breeding and breeding.

Oceanography in the Indian Ocean is strongly impacted by the central Pacific, with Indian Ocean warming occurring during ENSO warm phases (Blunden et al. 2011). Atmospheric teleconnections as well as large-scale oceanographic processes are thought to be responsible for the close connection between the Indian and Pacific Oceans (Klein et al. 1999). The year 2009 and early 2010 were characterized by the development and maturing of a strong El Niño event in the tropical Pacific (Lee & McPhaden 2010; Arndt et al. 2010). This El Niño event has been classified as a Central Pacific (CP) El Niño (Lee & McPhaden 2010), or El Niño Modoki (Ashok et al. 2007), which distinguishes it from the classical Eastern Pacific (EP) El Niño; this is characterised by the maximum warm SSTA located in the central and not the eastern equatorial Pacific. The 2009/10 El Niño has been shown to possess unique characteristics, such as the highest SSTA in the central equatorial Pacific, and has therefore been classified as the strongest CP El Niño for 30 years (Lee & McPhaden 2010). Moreover, atmospheric teleconnections and remote impacts of CP El Niño events are thought to be different from the “classical” EP El Niño (Ashok et al. 2007; Weng et al. 2007; Kug et al. 2009), but are less well studied and less well documented. The breeding season 1997/98 was characterized by the occurrence of a pronounced El Niño, but of the EP type. The less extreme impacts on king penguins at Kerguelen of this El Niño may have resulted from the different patterns of EP and CP El Niño events, and their different remote impacts. This hypothesis is not investigated further here, so remains somewhat speculative. However, projected environmental change in the Indian Ocean, with warming (Luffman et al. 2009) and increasing intensity (Lee & McPhaden 2010; Ren & Jin 2011) and frequency (Yeh et al. 2009) of the CP El Niño may indicate that the breeding season 2009/10 is a potential indication of future trends in the Indian Ocean and possibly also in the area around Kerguelen.

5.5.2.2 Connections to regional atmospheric processes: Cumulative effect of storm and warm anomalies in the South Indian basin

The extreme and temporally restricted nature of the oceanographic anomaly at Kerguelen during February 2010, and the occurrence of behavioural anomalies in king penguins only at Kerguelen but not at Crozet, suggests that forcing local to the area around the Kerguelen Plateau may have played a major role in addition to potential effects of larger-scale phenomena such as ENSO, potentially transferring and/or amplifying the larger-scale signal from the Indian Ocean to Kerguelen. In early February 2010, SLP and wind patterns indicated the passage of a pronounced storm in the Kerguelen area. Oceanography around the Kerguelen Plateau has been shown to be significantly impacted by local wind stress, with time lags of only several days (Meredith et al. 2004). High-frequency atmospheric anomalies such as storm events are therefore likely to have significant and immediate impacts on the local oceanography around Kerguelen. Wind stress plays an important role in the transport of water masses, creating Ekman transport of the upper ocean layer in 90° (to the left in the Southern Hemisphere) of the wind direction (Brown et al. 2001; Stewart 2008). The easterly wind anomaly from the storm in the Kerguelen area during early February 2010 may have created a southward Ekman transport of warm more northerly Indian Ocean waters to the Kerguelen Plateau. Such anomalous Ekman transport, due to local wind forcing, may have transferred the remote impacts of El Niño from the subtropical Indian Ocean to more southerly latitudes, possibly amplifying the effects of the El Niño in the Kerguelen area.

In addition to changes in Ekman transport, storms are known to have significant immediate impacts on the upper ocean (Kraus & Turner 1967; Black & Dickey 2008), which may have important consequences for the thermal structure of the water column and associated prey resources for king penguins. Wind stress may increase vertical mixing in the upper

water column (Kraus & Turner 1967), which may have enhanced the intrusion of the warm surface waters into the upper ocean. Heat transfer from the SML to the thermocline by increased turbulent mixing may lead to a warming of the upper thermocline (Black & Dickey 2008). This may have reduced the suitability of the thermocline and adjacent water masses, such as the SML and WW, for myctophids, as shown by the lower foraging performance of king penguins associated with the SML, TH and WW in 2010. Storm passage in the open ocean is known to cause local deepenings of the SML (Black & Dickeney 2008) and may also deepen the underlying water masses, such as the thermocline and WW, which are key features for foraging king penguins (see Chapter 4). In addition to changes in prey distribution, due to the warming of the water column, a deepening of these upper water masses may imply higher dive efforts for foraging king penguins to reach associated prey resources; this was indicated by the deeper bottom start depths in 2010. Increased vertical mixing by the storm may furthermore decrease the stratification of the water column (Black & Dickey 2008; Ropert-Coudert et al. 2009b), and local warm-water intrusions, SML deepenings and thermocline warmings, leading to irregularity in the water column structure, as shown by the TDR temperature profiles. Such a loss of structure in the water column may lead to the dispersion of myctophids associated with specific water masses or thermal features (Charrassin & Bost 2001; Scheffer et al. 2012). Ropert-Coudert et al. 2009 suggested reduced prey availability for little penguins in mixed waters, which may also be the case for king penguins.

Storms have been reported to cause important oceanographic and ecological disturbances in various ocean systems (Paine et al. 1998; Yang et al. 2004; Black & Dickey 2008), and to impact higher trophic levels such as marine predators (Ropert-Coudert et al 2009; Lea et al. 2009). Local amplification by storm activity of ENSO-related effects on oceanography and marine ecosystems occurred during the strong El Niño events in 1982/83 (Paine et al. 1998) and 1997/98 (Napp & Hunt 2001). In February 2010, the combined effect of the

Indian Ocean warming by El Niño together with the southward warm-water transport and changes in the water column by the storm passage may have led to oceanographic disturbances in the area around Kerguelen that significantly impacted king penguins' foraging. Ecosystem disturbances through such amplified effects of perturbations may be of higher amplitude than anticipated and result in "ecological surprises", as ecosystem responses may be multiplicative and not additive (Paine et al. 1998). King penguin trip duration (Le Maho et al. 1993), and marine predator behaviour in general (Weimerskirch et al. 2003; Costa et al. 2010), may be considered as plausible indicators of the marine ecosystem, suggesting that the extreme behavioural and reproductive anomalies of king penguins were an ecosystem response with increased amplitude at Kerguelen in 2010. The amplification effect of environmental conditions may be one of the crucial differences to the 1997/98 breeding season, when king penguins breeding at Kerguelen did not show any comparable anomalies in foraging and breeding success despite the occurrence of the strong El Niño. Although there are no consistent predictions about the future frequency of storm occurrences (Meehl et al. 2000; Webster et al. 2005; Emanuel et al. 2008), it has been suggested that it will increase in the south Indian Ocean with Indian Ocean warming (Xie et al. 2001; Luffman et al. 2009). This may mean increased risks of similar perturbations on the Kerguelen ecosystem, potentially amplifying the signatures of larger-scale environmental variability, or locally altering water column properties.

5.5.3 Biological significance of the 2010 event

The breeding season of 2009/10 was characterized by behavioural and reproductive anomalies for king penguins of unprecedented extent, when compared with any year since the start of the long-term monitoring programme at Kerguelen (1998). Environmental variability is known to impact penguins (see review in Forcada & Trathan 2009; Bost et al.

2011; Peron et al. 2012) as well as other seabirds (Weimerskirch et al. 2003; Jenouvrier et al. 2005; Frederiksen et al. 2008; Barbraud et al. 2011) as well as other marine predators across the Southern Ocean (Murphy et al. 2007; Trathan et al. 2007; Costa et al. 2010). However, environmental change occurs on different temporal and spatial scales, ranging from large-scale background signals to small-scale weekly or daily events. In addition to long-term changes in the mean climate, small-scale weather events may significantly alter environmental conditions and possibly amplify the effects of larger-scale modes of environmental variability or climate change. Non-linear ecosystem responses to the amplified effect of multiple disturbances (Paine et al. 1998; Meehl et al. 2000) as well as complex air-sea and ecosystem interactions may make the modelling-based prediction of the impacts of future environmental variability on ecosystems and marine predators difficult.

Extreme anomalous events have the potential to allow insights into reactions of ecosystems and specific components to extreme conditions, which may indicate potential reactions and adaptations to future environmental change (Trathan et al. 2007; Forcada & Trathan 2009; Peron et al. 2012). Extreme events are characterized by their unproportional effects compared with their short duration, measured by statistical extremity with respect to a given historical reference period and by the abruptness relative to the life cycles of the organisms affected (Jentsch et al. 2007, see Figure A1). At Kerguelen, behavioural indices such as trip duration, distance travelled and diving behaviour, reproductive success and environmental parameters targeted during the penguins' foraging trips, as well as environmental conditions local to the foraging area and at larger scales regarding the CP ENSO signal clearly exceeded records since the start of the Kerguelen king penguin monitoring programme in 1998 and mostly occurred at small temporal scales, suggesting the extreme nature of the breeding season 2009/10 in terms of environmental conditions as well as behavioural responses of king penguins breeding at Kerguelen.

Extreme events can push an ecosystem beyond the threshold of its dynamic equilibrium and lead to ecosystem regime shifts with new system trajectories (Scheffer & Carpenter 2003). However, less severe events not inducing such profound shifts may allow important insights into responses of different ecosystem components to extreme conditions. Examining the local and larger-scale environmental conditions causing extreme behavioural patterns may further allow the identification of key features or conditions that may be crucial for a given system or one of its components at local scales, and allow for the assessment of potential connections to larger-scale climate signals. Investigating the environmental conditions as well as the links between oceanography and behaviour leading to anomalies in king penguins' behaviour is therefore important for a better understanding of key elements in king penguins' foraging and reproductive success, and in order to better assess potential reactions about future environmental change.

Changes in the distribution of environmental parameters such as the mean and variance lead to non-linear changes in the frequency and amplitude of extreme events due to shifts in the distribution tails (Mehl et al. 2000; Jentsch et al. 2007). Ongoing climate change and future warming of the oceans (Gille 2002; Solomon et al. 2009), means extreme events are predicted to be more frequent (Jentsch et al. 2007; Solomon et al. 2007; Jentsch & Beierkuhnlein 2008). Intensification of weather extremes is currently emerging as an important aspect of climate change, and research on extreme events (event-focused in contrast to trend-focused) has increased in recent years (Jentsch et al. 2007). Investigating ecosystem or species reactions towards extreme events and evaluating critical environmental conditions where systems or components can not adjust, and the underlying causes for these critical points is an important issue. The 2010 event allows insights into key elements of successful foraging of king penguins breeding at Kerguelen, and into possible reactions towards pronounced changes in their foraging habitat.

Impact of extreme events on top predators ecology

Extreme weather events have been shown to negatively affect marine predators in the Southern Ocean, including factors such as the survival of fur seal pups (Lea et al. 2009) and seabirds (Frederiksen et al. 2008). For threatened seabirds, extreme events are thought to lead to higher probability of extinction through increasing process variance in survival (Frederiksen et al. 2008). Our study confirms the negative impact of extreme environmental events on king penguins breeding at Kerguelen in terms of foraging and reproductive success, which is ultimately impacting upon their survival. It therefore underlines the importance to including the impacts of extreme events and their increasing frequency (Solomon et al. 2007) into predicting the ecological effects of climate change as suggested by Frederiksen et al. (2008). At South Georgia, penguins and fur seals showed their lowest weaning and fledging masses on record during a local warm SST anomaly in the foraging area of these marine predators during the breeding season 2009 (Hill et al. 2009). Even though a warm year was expected from remote impacts (Meredith et al. 2008; Hill et al. 2009), the local warming was greater than expected, and predator data and a combined standard index suggest 2009 to be the worst year on record with only 1994 being comparable (Croxall et al. 1999; Hill et al. 2009). It has been suggested that the warm SST anomaly may have been caused by intense in-situ heating of the mixed layer as a consequence of local atmospheric effects (Hill et al. 2009). Such patterns of local upper-ocean warming and extreme effects on marine predators, potentially also through alterations in prey distribution, may be similar to the situation and mechanisms at Kerguelen during February 2010. At Kerguelen, other predator species feeding on myctophids may have been affected in a similar way as king penguins from the anomaly in 2009/10; however these species may not have been monitored during that period.

At Kerguelen in February 2010, the clear changes in patterns of oceanography and patterns of king penguin behaviour, appeared to be caused by the occurrence of strong large-scale signals of environmental variability (El Niño + Indian Ocean warming) in combination with the smaller-scale atmospheric anomaly in the foraging area (storm passage). Drastic southward shifts in key oceanographic features in the area to the south and south-east of Kerguelen presumably induced significant changes in upper water column properties, and therefore in prey resources for king penguins. The PF position in the area to the south-east of Kerguelen seems to play a critical role by significantly impacting the cold-water influx from the FTC over the Chun Spur, which is thought to be of considerable importance for the structure of the oceanographic habitat in the area to the south-east of Kerguelen, and therefore for king penguin foraging. Shifts in the horizontal and vertical foraging habitat as well as significant increases in foraging effort at the surface and at depth indicate the behavioural responses of king penguins to the extreme anomaly. However, even though body mass gains indicate success in terms of adult survival, the exceptionally low reproductive success shows that the behavioural adaptations towards the extreme environmental conditions were not successful in terms of offspring survival. Long-lived species such as king penguins integrate across years when events of low reproductive success occurred. However, such complete breeding failure as reported for king penguins at Kerguelen in 2009/10 may impact future population development, and should be a subject of future monitoring work at Kerguelen.

Southward shifts of the PF as well as oceanic warming are expected to increase in the future (Solomon et al. 2009). Therefore, the breeding season of 2009/10, as a year of historical highs for Indian Ocean SST (Blunden 2011), may provide valuable insights into the potential consequences of the projected continuing warming of the Indian Ocean (Luffman et al. 2009). Although there is no consensus about the general impact of climate change on future storm activity (Meehl et al. 2000; Webster et al. 2005; Emanuel et al.

2008), storm tracks in the southern Indian Ocean are thought to be enhanced with continued warming (Luffman et al. 2009) through increases in meridional temperature gradients and release of latent heat in baroclinic eddies (Luffman et al. 2009), as well as through down welling of El-Niño generated Rossby waves (Xie et al. 2001). The 2010 event may therefore allow insights into the potential consequences of the projected future warming, particularly southward shifts of the PF and/or increased occurrences of extreme events such as storms events on king penguins breeding at Kerguelen. The reduced suitability of the area near to the Kerguelen Plateau for king penguin foraging, resulting in increased time and energy requirements, as well as in their exploration of potentially less stable oceanographic features in the open ocean, illustrates the negative effects of the extreme environmental situation on king penguins. These consequences may be important for other marine predators feeding near to the Kerguelen Plateau, particularly those that use similar areas and oceanographic structures for foraging, and are dependent on similar oceanographic and atmospheric processes (Hindell et al. 2011).

Additional figures (from other publications):

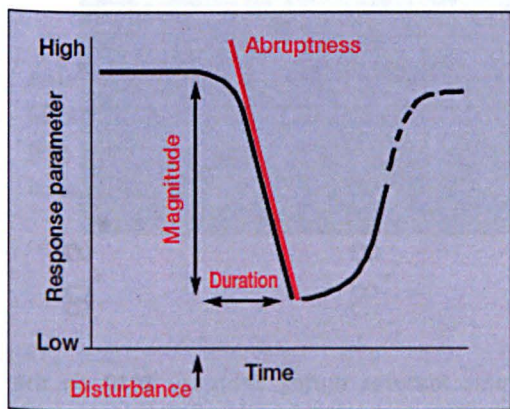
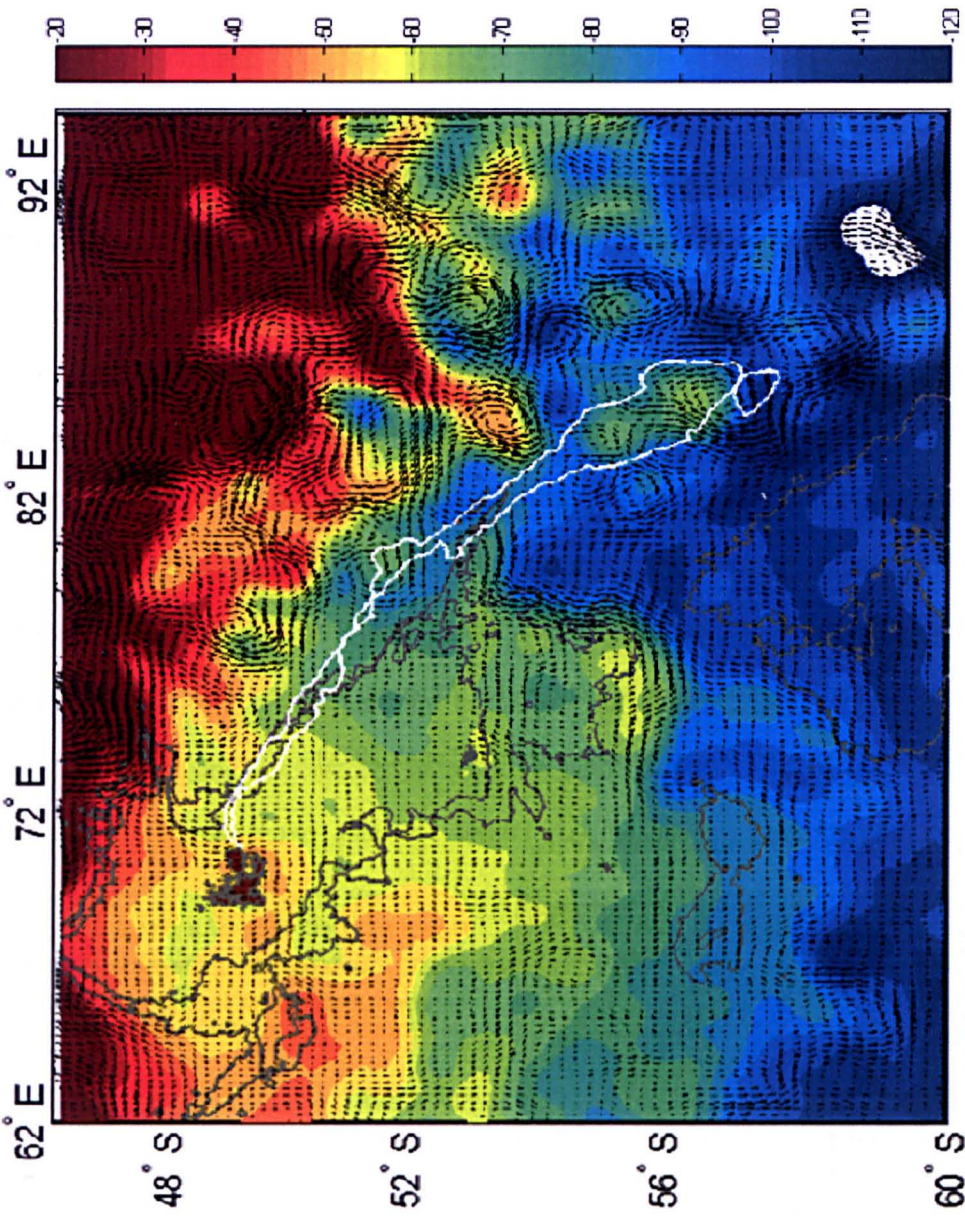


Figure 4. Test of a discrete event: abruptness. The abruptness of an event is a function of magnitude over duration. Note that magnitude of the disturbance event refers to its effect on the parameter studied, such as destruction of biomass. Duration of the disturbance event is to be perceived relative to the lifespan of the organisms studied (White and Jentsch 2001).

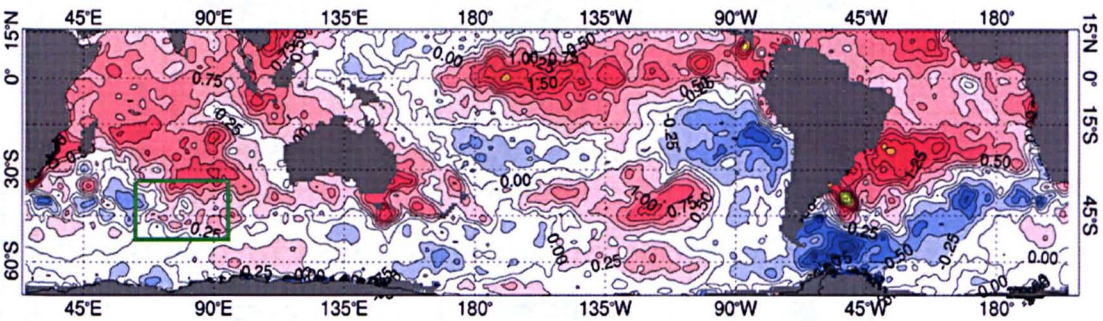
Figure A1: Definition of a discrete abrupt event, defined by magnitude over duration. Figure from Jentsch et al. (2007).

Annexes Chapter 5:

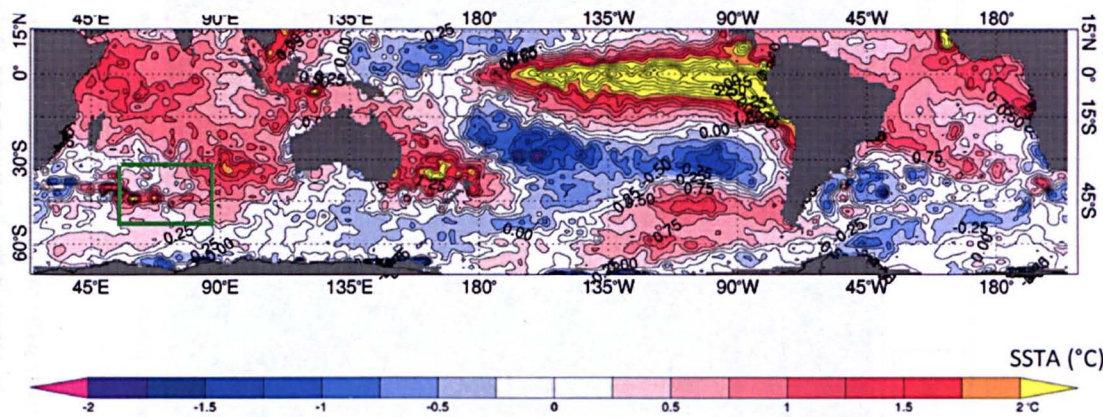


Annex A: Exploration of offshore oceanographic features during February 2010 on the example of one penguin (shown in white). Colours indicate SSH, arrows direction and intensity of the geostrophic current. Grey lines show bathymetry at 0,1000 and 2000 m depth. SSH and geostrophic velocities represent oceanography during 4 days in the Middle of the foraging trip, when the bird foraged in proximity of the warm-core oceanographic feature in the south. Data source for SSH and geostrophic velocities: Aviso.

(b) – February 2010



(a) – February 1998



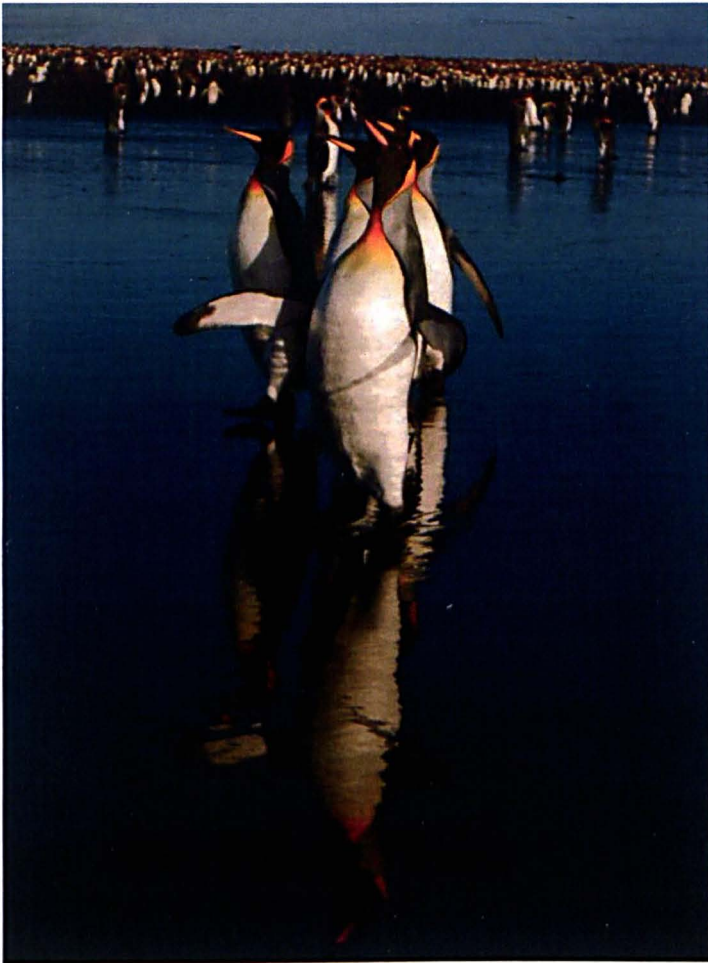
Annex B: Monthly SSTA maps for February a – 2010 and b - 1998. In the equatorial Pacific warm SSTA show the typical El Nino signature for a - Central Pacific (CP) El Nino, and b – Eastern Pacific (EP) El Nino. The green boxes indicates the study area around Kerguelen. Data source: HadISST1 dataset, Met Office.



Annex C: Daily snapshots of Mean Sea Level Pressure anomaly patterns in the southern Hemisphere from 25 January – 6 February 2010, Illustrating the development of the high-low pressure system causing the storm in the Kerguelen area. Data source: NOAA NCEP.

Chapter 6

Impact of environmental variability on the foraging behaviour of king penguins breeding at Kerguelen



6.1 Abstract

In the marine environment, variability in mesopelagic conditions is known to influence the distribution of mid-trophic level species which are prey for diving predators, including king penguins. Investigating the behavioural responses of marine predators to variability in key oceanographic features is crucial for our understanding of the animals' foraging strategy, and how they might cope with future environmental change.

In this study we examined the foraging behaviour of king penguins breeding at Kerguelen (south Indian Ocean) in relation to variability in oceanographic features in their foraging area, and how birds may adapt to variability in such features. We used ARGOS and Global Positioning System (GPS) tracking together with Time-Depth-Temperature-Recorders (TDR) to follow the at-sea movements of king penguins. Combining observed penguin behaviour with oceanographic data at the surface through satellite data and at depth through in-situ recordings by the penguins enabled us to explore how such predators adjust their horizontal and vertical movements in response to variability in their physical environment.

The position of the Polar Front (PF) and its interaction with the cold-water influx from the Fawn Trough Current (FTC) to the south-east of Kerguelen appeared to be of key importance for mesopelagic foragers such as king penguins, indicated by adjustments in their foraging trip duration as well as diving behaviour following movements of these oceanographic features. Southward shifts in the PF and FTC positions, resulting in a reduction of the cold-water influx over the Chun Spur into the penguins' foraging area, lead to significant increases in foraging trip duration extending into Antarctic Zone (AAZ) and Southern Antarctic Circumpolar Current Front (SACCF) waters, as well as to increased exploration of Circumpolar Deep Water (CDW) at depth.

Our study indicates that the FTC influx into the area to the south-east of Kerguelen and its interaction with the PF and the Kerguelen Plateau bathymetry plays a key role for foraging king penguins. Southward shifts in this cold-water flux appear to result in reduced foraging habitat profitability of the immediate Kerguelen Plateau area to king penguins, indicated by reduced use of areas related to the Kerguelen Plateau bathymetry, and increased exploration of offshore oceanographic features of higher geostrophical velocities and more southern surface signatures as well as by the exploration of water masses of southern origin at greater depth.

6.2 Introduction

Environmental variability is known to impact oceanography at the surface and in the water column, therewith influencing the distribution and abundance of prey for upper trophic levels such as marine predators. Assessing of the potential impact of environmental variability and climate change on marine predators requires the identification of the key oceanographic features and the processes on which the animals rely for foraging/which the animals explore during foraging as well as information about how these oceanographic features are varying over time, and how they are likely to change in the future (Lea & Dubroca 2003; Weimerskirch et al. 2003; Jenouvrier et al. 2009; Costa et al. 2010).

King penguins are important avian predators of the Southern Ocean (Woehler 1995; Bost et al. 2012). They rely mainly on myctophids (Myctophidae: lantern fish) (Cherel & Ridoux 1992), mesopelagic fish that are generally associated with particular water masses or temperature ranges (Hulley 1981; Kozlov et al. 1991) as well as with fronts and related oceanographic features (Brandt et al. 1981; Pakhomov et al. 1996; Rodhouse et al. 1996). The horizontal and vertical distribution of water masses is therefore of key importance for foraging predators such as king penguins. King penguins are known to explore their

foraging habitat in a non-random way, targeting large- and mesoscale surface features such as fronts and eddies (Cotté et al. 2007; Trathan et al. 2008; Scheffer et al. 2010) as well as specific water masses and thermal features within the water column (Charrassin & Bost 2001; Scheffer et al. 2012) during prey search. However, we still have little knowledge about how king penguins may adapt to variability in these oceanographic features explored during foraging.

During the summer breeding season, king penguins have important time and energy constraints, arising from their need to regularly return to their colony to relieve their incubating partner or provision their chick (Charrassin et al. 1998, 2002; Halsey et al. 2010). The breeding success of central-place foragers such as king penguins therefore critically depends upon the quality and quantity of food gathered by the parents as well as upon their efficiency in exploring the prey resources within their foraging ambit (Weimerskirch 2007). Such factors will contribute towards determining their foraging trip duration as well as their exploration of the foraging habitat at the surface and at depth.

The Kerguelen archipelago is located within the flow of the Antarctic Circumpolar Current (ACC) in the south Indian Ocean, with the Sub-Antarctic Front (SAF) situated to the north and the Polar Front (PF) and Fawn Trough Current (FTC) to the south. The most prominent oceanographic features in the area to the south-east of Kerguelen are the Polar Front (PF) and the Fawn Trough Current (FTC), both of which are part of the ACC. The PF has been identified to flow eastwards across the northern Kerguelen Plateau just south of Kerguelen (Park et al. 1998; Charrassin et al. 2004; Park et al. 2008b, Park & Vivier 2011), then wraps anticyclonically around the island from the south-east to continue its flow north-eastward, and then flows again south-eastwards along the east of the Kerguelen Plateau (Park & Vivier 2011). The FTC is a strong current flowing along the southern edge of the Northern Kerguelen Plateau through the Fawn Trough, a deep passage (<2800 m)

separating the Southern and the Northern Kerguelen Plateau and channelling an important part of the ACC flow (Park et al. 2008b; Roquet et al. 2009). The cold WW advected from the Fawn Trough over the Chun Spur flows northwards along the eastern shelf break of the Kerguelen Plateau, forming a cold-water subsurface tongue that can extend up to the latitude of Kerguelen (Charrassin et al. 2004; Park et al. 2008b; van Wijk et al. 2010), where it reaches depths of ~100 m (Charrassin et al. 2004). Its northward extension appears to be variable, but the factors affecting the flow are not well understood.

King penguins are one of the most important avian predators breeding at Kerguelen (Bost et al. 2012), comprising an estimated 342 000 breeding pairs, quickly increasing (Chamailé-Jammes et al. 2000; Bost et al. 2012, last estimate dating to 1999). During the summer season, king penguins generally explore the area to the south-east of Kerguelen during their incubation, brooding and crèche foraging trips (see Chapter 4; Koudil et al. 2000; Charrassin et al. 2002; Bost et al. 2002; Pütz et al. 2002; Charrassin et al. 2004; Bost et al. 2011; Hindell et al. 2011), where the subsurface tongue of cold water originating from the FTC and its juxtaposition with the PF have been shown to be of key importance for the foraging penguins (see Chapter 4; Charrassin et al. 2002; Charrassin et al. 2004). However, there is currently no knowledge about how penguins may adapt to changes in these key oceanographic features, and what may be their limits of flexibility in foraging behaviour to buffer such variability.

King penguins are thought to be vulnerable to environmental variability (Le Bohec et al. 2008; Bost et al. 2011; Péron et al. 2012); although most such studies have not explored how king penguins utilise the water column and instead have relied upon studies based on surface behaviour. However, diving predators such as king penguins critically rely upon a 3-dimensional habitat, and so are impacted by oceanographic conditions in both the horizontal and vertical dimensions. In order to better understand the foraging behaviour of

penguins and other diving predators, and to evaluate the potential impacts of environmental change on an animals' behaviour and survival, changes in vertical habitat descriptors and the impact on the animals' behaviour must be taken into account (Costa et al. 2010; Hindell et al. 2011). The use of in-situ oceanographic data collected by animal-borne devices in combination with surface tracking allows us to study the movements of diving predators in their 3-dimensional habitat and to investigate how environmental conditions encountered in the horizontal and vertical dimension may impact the animals' behaviour (Costa et al. 2010; Hindell et al. 2011).

In this study we investigated the foraging behaviour of king penguins breeding at Kerguelen in relation to variability in oceanographic conditions within their foraging area. We explored interannual differences in foraging behaviour at the surface and at depth in relation to changes in key oceanographic features in their foraging area which have been shown to be explored during foraging (see Chapter 4). In this context we particularly investigated the impact of changes in the PF position the northward extent of the FTC influx into the penguins' foraging area, both of which have been shown to be important features explored by foraging king penguins at Kerguelen (see Chapters 4 and 5).

6.3 Material and Methods 3

6.3.1 Study area, study period and device deployments

Study area, study period and device deployments correspond to those described in Chapter 4.

6.3.2 Environmental data

Environmental data used (bathymetry and slope, remotely sensed oceanographic as well as vertical temperature data and water mass definition) correspond to those described in Chapter 5.

6.3.3 Data analysis:

Data analyses were performed using Matlab (The MathWorks, Inc., MA 01760-2098, USA) and the custom-made software MultiTrace (Jensen software systems, Laboe, Germany).

6.3.3.1 Analysis of surface behaviour:

Processing of the Argos and GPS data was carried out as described in Chapter 4, using the process model of state space models for the Argos data. First-passage time analysis was applied to the surface tracking data to identify foraging behaviour (see Chapter 4 for a more detailed description). For each location we assigned SSH, geostrophic velocity, bathymetry and slope values by searching for the geographically nearest value within the corresponding dataset. Surface locations were then assigned to frontal classes (PFZ, PF, AAZ, SACCF) based on SSH signatures following Venables et al. (2012), and to bathymetry classes based on depth and slope. Bathymetry classes were defined as shelf (depth ≤ 1000 , slope < 0.2), shelf break (depth $> 1000\text{m}$, slope ≥ 0.2) and offshore (depth > 1000 , slope < 0.2).

For each bird, we calculated the trip duration from the Argos and GPS data. Exact departure and return times from and to the island were determined from the TDR data for birds with Argos/GPS and TDR devices, and from field observations and visual inspection of surface tracks arriving at the colony for Argos/GPS data only.

6.3.3.2 Analysis of diving behaviour:

A zero offset correction was applied on the dive data. Only dives deeper than 50 m depth were used for analysis, as they were considered to represent the majority of king penguins foraging dives (Pütz et al. 1998; Charrassin et al. 2002).

Diving behaviour and the use of the water column by the penguins while foraging was analysed by considering the bottom phase and wiggle numbers of the dives, as the bottom phase is thought to be the most important phase for prey capture (Charrassin et al. 2002, Simeone & Wilson 2003; Ropert-Coudert et al. 2006), and wiggles have been shown to be reliable indicators of prey capture by king penguins (Simeone & Wilson 2003; Takahashi et al. 2004; Bost et al. 2007; Hanuise et al. 2010). The duration of the bottom phase was defined as the time between the first and last wiggle or dive step deeper than 75% of the maximum dive depth, following Halsey et al. (2007), and the number of wiggles as deviations >1 m of depth with an absolute vertical instant greater than 0 as a reliable proxy of feeding success (Bost et al. 2007; Hanuise et al. 2010).

Vertical profiles of diving behaviour and in-situ thermal properties of the water column were calculated as described in Chapter 4.

The relative bottom time spent in a specific water mass was calculated as the proportion of the total bottom time of the dives spent in the particular water mass. This allowed the evaluation of the importance of a water mass for prey pursuit. Comparisons of the relative Circumpolar Deep Water (CDW) bottom times at different PF and FTC positions allowed to assess how birds explored the water column depending on the frontal positions.

As king penguins are visual feeders and essentially forage during the daylight and twilight hours (Bost et al. 2002), night dives were excluded from these analyses (corresponding to 16.7% of the total dives < 50 m depth, and 2.1% of the total dives > 50 m depth. However,

for birds equipped with TDR devices only, geographical coordinates of the dives could not be calculated. For the approximate identification of sunrise and sunset, and the consequent discharge of night dives from the analysis, we used the sunrise time at the easternmost and sunset time at the westernmost point reached by the foraging trips. This method allowed to exclude night dives from the analysis while being conservative for twilight hours, leading to including some night dives into the analysis instead of possibly discharging twilight dives if sunrise and sunset times were set too late or early, respectively.

6.3.3.3 Identification of frontal positions in the foraging area

We used frontal positions in the area to the south-east of Kerguelen to characterize oceanographic conditions in the king penguins' foraging area. Surface positions of oceanographic features, particularly of the PF, can be determined from different parameters such as SST (Orsi et al. 1995; Park et al. 1998b; Moore et al. 1999b) or SSH (Sokolov & Rintoul 2009; Venables et al. 2012). In our study, indices of frontal positions in the area to the south-east of Kerguelen were determined from SST signatures, as SST provided the best surface evidence for shifts in the FTC from visual inspections of the SST and SSH signature maps (see Chapter 5, Figures 5.8 and 5.9). The PF surface signature was defined 4°C from SST, corresponding to the southern boundary of the 4-5°C PF signature (Park et al. 1998). As there are contrasting definitions of the FTC surface signature in the literature (Park et al. 1998; van Wijk et al. 2010; Park & Vivier 2011), the SST signature for the FTC was determined as the 11-year means of SST in the Fawn Trough canyon from 1998-2009, thus characterizing the surface expression of the flow through the Fawn Trough without making pre-assumptions about frontal assignments. The frontal positions were determined in the area between 55-60°S, 80-82°E, where the FTC reaches its northernmost position to the south-east of the Kerguelen Plateau and

approaches the PF above the Chun Spur. The PF position was defined as the southernmost position of the 4°C contour, and the FTC position as the northernmost position of the 1.6°C contour within the defined area.

6.3.3.4 Relations between frontal positions (Polar Front and Fawn Trough Current) in the foraging area

To investigate the spatial variability of the FTC with the PF position in the area to the south-east of Kerguelen, we plotted daily FTC against PF positions for the period of February 1998 - 2011. Mean and percentiles of PF positions at the 5% and 95% level were determined for the FTC position being located to the north and the south of the Chun Spur in order to identify threshold PF positions of the FTC switching to the south of the Chun Spur. We used linear regression to quantify relations between the PF and FTC position for the FTC being located to the N or the S of the Chun Spur.

6.3.3.5 Impact of frontal positions on foraging behaviour and foraging habitat exploration

To investigate the impact of frontal positions on the penguins' foraging behaviour at the surface and at depth we compared the horizontal foraging habitat use (bathymetric and frontal classes explored during foraging) and the diving behaviour (number of wiggles per dive and the exploration CDW within the water column) at different PF and FTC positions characterizing the situation of the FTC being located i) to the north of the Chun Spur, ii) to the south of the Chun Spur, or iii) to the north or the south of the Chun Spur. Comparisons of the penguins' behaviour at the different frontal positions were carried out using Kruskal-Wallis tests as tests for normality failed (Jarque Bera test) and transformations did not help the data to conform to the normality assumption. When significant differences were found

among groups, an all pairwise multiple comparison (Dunn's method) was performed to determine the groups that differed from the others. Relations of the penguins' foraging trip durations and body mass gain during incubation and brooding with the PF position were investigated using linear and quadratic regression.

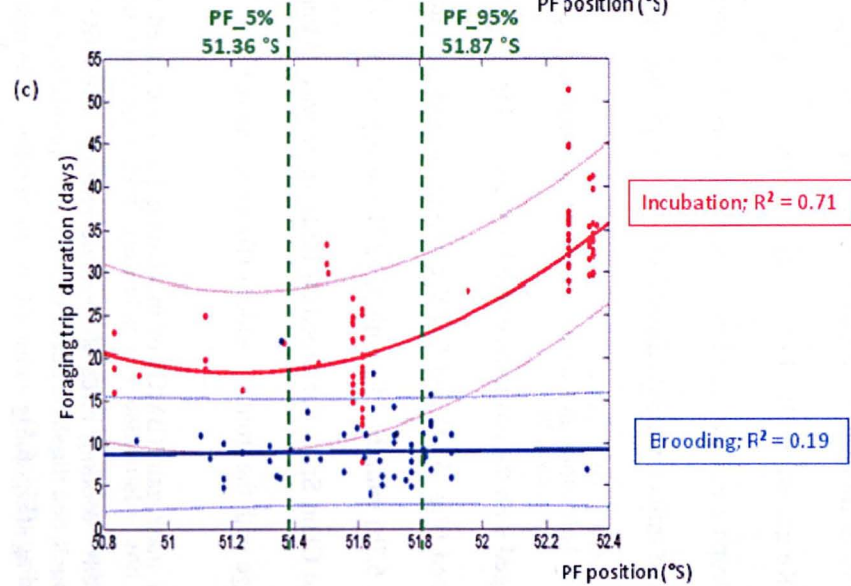
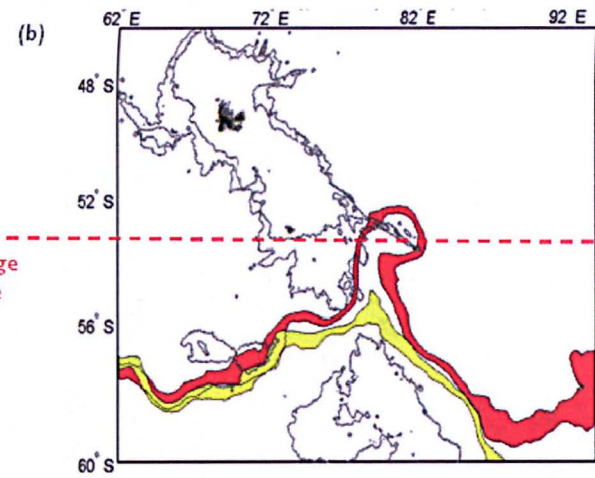
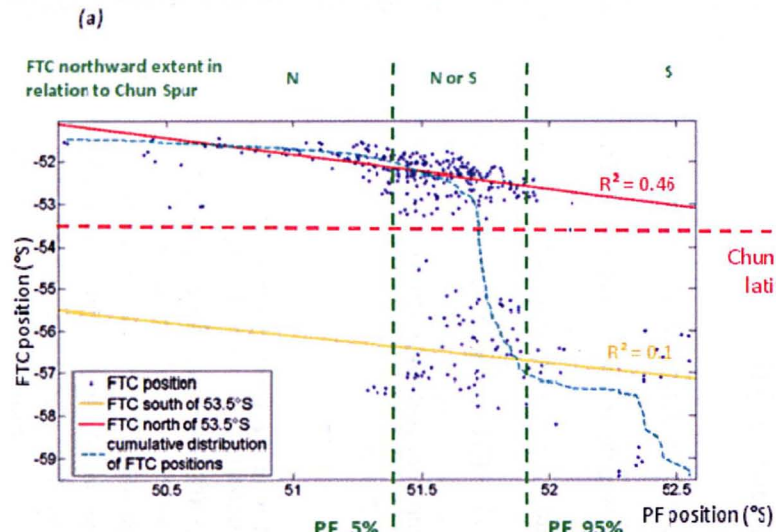
6.4 Results

6.4.1 Interactions and variability of oceanographic features in the area to the south-east of Kerguelen

The PF and FTC positions based on SST signatures in the Chun Spur area showed linear relationships with FTC positions north of 53.5°S (Fig. 6.1a). Abrupt southward shifts of FTC positions occurred from PF positions of 51.2°S, leading to a loss in linearity between the PF and the FTC positions ($R^2 = 0.46$ if FTC north of 53.5°S; $R^2 = 0.1$ if FTC south of 53.5°S).

Spatial patterns of the FTC surface signature overlaid on the Kerguelen Plateau bathymetry illustrates that the break in linearity corresponds to the FTC shifting to the south of the Chun Spur, with the surface patterns of FTC waters changing from looping northward over the Chun Spur to a straight flow through the FT canyon, leading to abrupt and non-linear shifts in FTC position latitudes (Fig. 6.1b).

Figure 6.1 (next page): Oceanographic interactions between the Polar Front (PF) and the Fawn Trough Current (FTC) in the south-east of Kerguelen during February 1998-2011. a – Position of the FTC in relation to the PF position in the area to the north of the Chun Spur. Frontal positions are determined from SST surface signatures: the northernmost position of the 1.6°C isotherm for the FTC, and the southernmost position of the 4°C isotherm for the PF (a detailed description is given in M&M). Green lines indicate the 5% and 95% percentiles of the FTC positions being shifted to the south of the Chun Spur. b – Spatial patterns of the FTC surface signature from SST, with the FTC looping to the north of the Chun Spur (red), and shifted to the south of the Chun Spur (yellow), illustrating the non-linearity of FTC shifts to the south of the Chun Spur. c - Trip duration of incubating (red) and brooding (blue) birds in relation to the Polar Front (PF) position derived from SST data. Dotted lines represent prediction boundaries at a confidence level of 0.95. Data source SST data: Met Office.



6.4.2 Foraging behaviour and body mass gain in relation to frontal positions

Trip duration of incubating birds increased with the southward position of the Polar Front ($R^2=0.71$) (Fig. 6.1c). Foraging trip duration showed increases from PF positions south of 51.36°S , where FTC shifts occurred.

The penguins' horizontal foraging habitat regarding bathymetric features and oceanographic properties changed with the PF position (Fig. 6.2). Both incubating and brooding birds showed decreased exploration of shelf break areas, with incubating birds increasing foraging in offshore regions, and brooding birds increasing the exploration of the Kerguelen shelf (Fig. 6.2a). Incubating birds showed shifts towards increased geostrophic velocities and more southern SSH signatures until the SACCF. Brooding birds showed shifts towards warmer SST with the PF moving southwards (Fig. 6.2b).

Diving behaviour and water masses exploration during bottom periods of incubating birds changed with the positions of the Polar Front (Fig. 6.3). Wiggle numbers were significantly reduced (Fig. 6.3a) and CDW exploration during bottom periods significantly increased (Fig. 6.3b) with the PF south of 52°S , corresponding to the FTC being shifted to the south of the Chun Spur. For brooding birds, there was no apparent pattern of diving behaviour change with the frontal positions (figure not shown).

Body mass gain (BMG) of incubating birds increased with the south position of the PF, whereas brooding birds showed decreasing BMG ($R^2=0.29$ for incubation, $R^2=0.36$ for brooding) (Fig. 6.4).

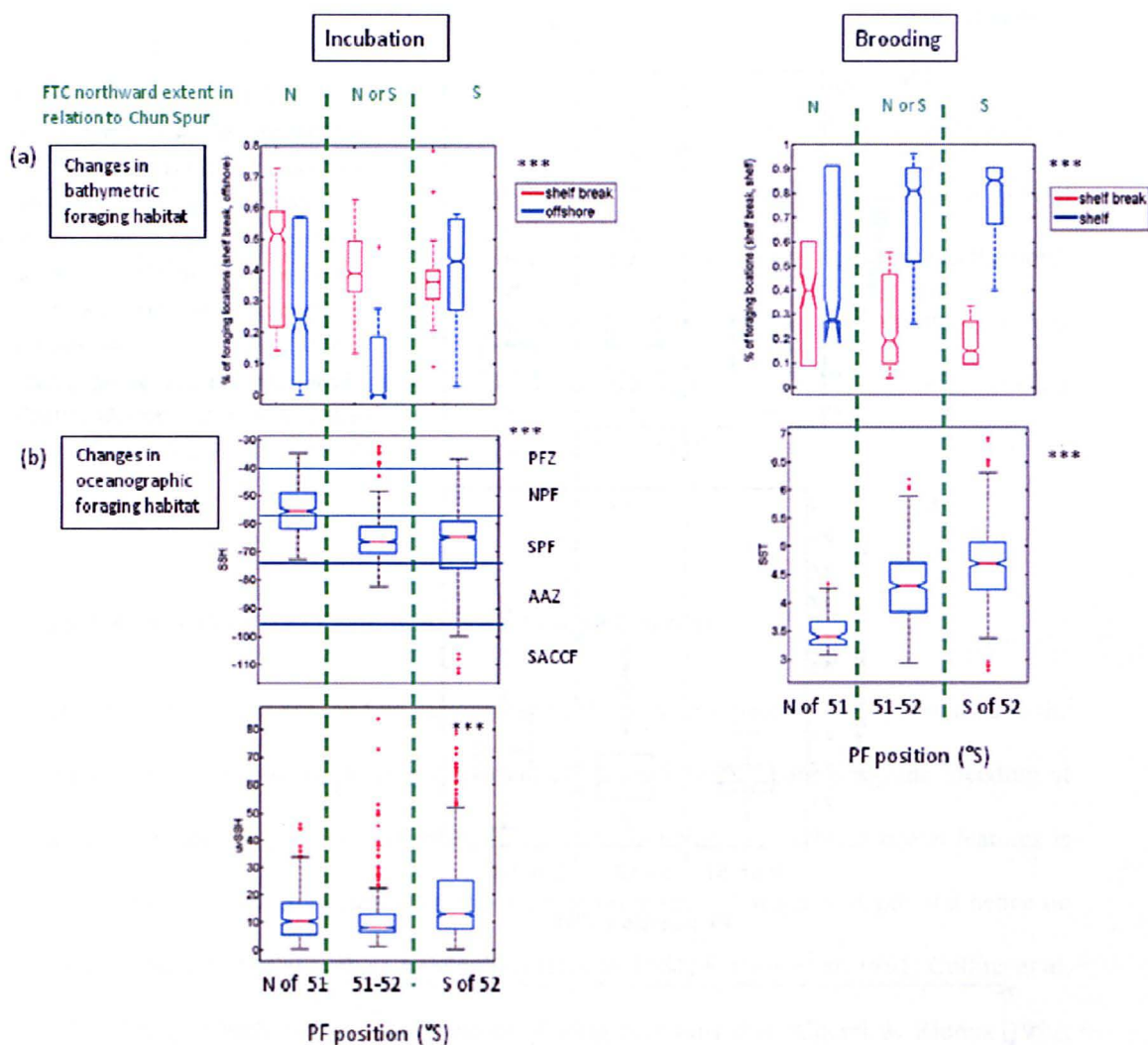


Figure 6.2: Changes in horizontal foraging habitat regarding a - bathymetry and b - oceanography (SSH, geostrophic velocities, SST) of incubating and brooding penguins. Bathymetry classes (shelf, shelf break, offshore) were defined based on depth and slope, see M&M for details. *** indicate significant differences to the other groups with $p = 0.01$ (Kruskal-Wallis Test), if placed next to the boxplot figure, all groups showed significant differences to the others. PFZ: Polar Frontal Zone; PF: Polar Front; AAZ: Antarctic Zone; SACCF: Southern ACC Front.

FTC northward extent in relation to Chun Spur

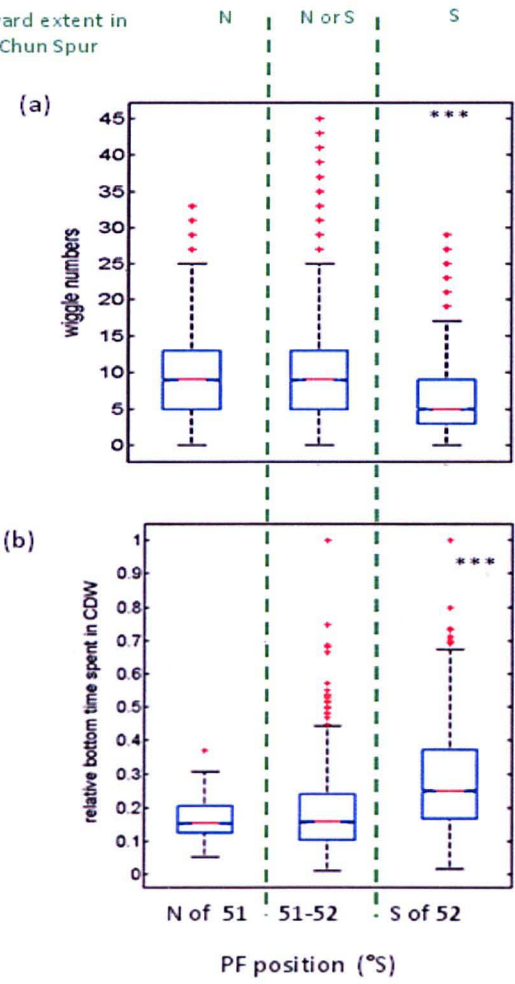


Figure 6.3: Changes in diving behaviour of incubating birds with the positions of the PF. a – number of wiggles; b – relative bottom time spent in CDW (= bottom time in CDW / total bottom time for each dive >50m depth). *** indicate significant differences to the other groups with $p = 0.01$ (Kruskal-Wallis)

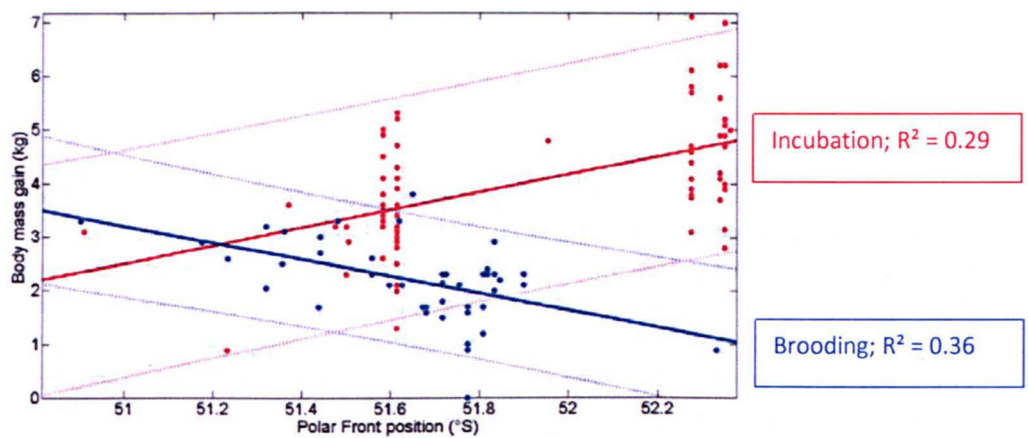


Figure 6.4: Total body mass gain of incubating (red) and brooding (blue) birds in relation to the Polar Front position. Dotted lines represent prediction boundaries at a confidence level of 0.95.

6.5 Discussion

6.5.1 Response of a diving marine predator to oceanographic variability

The foraging behaviour of king penguins breeding at Kerguelen showed significant responses to environmental variability in their surface travel and diving behaviour as well as body mass gain. Regional variability in oceanographic conditions in the area to the north of the Chun Spur appeared to be of key importance for changes in foraging of diving predators such as king penguins, with southward shifts in the PF and FTC surface signatures negatively impacting the penguins' foraging efficiency.

6.5.2 Role of the Polar Front and Fawn Trough Current

The PF and the FTC are the two major large-scale oceanographic features in the area to the south-east of Kerguelen, playing important roles for foraging king penguins breeding at Kerguelen (see Chapter 4). Variability in surface characteristics of these ocean features is likely to have important impacts on the thermal properties of water at depth and hence on the distribution of prey such as myctophids (Hulley 1981; Kozlov et al. 1991; Collins et al. 2008, 2012), which are key components of king penguins diet (Cherel & Ridoux 1992; Bost et al. 2002).

The area downstream of the Kerguelen Plateau is characterized by the presence of different ACC fronts (Park et al. 1998; Park et al. 2008b; Sallée et al. 2008; Roquet et al. 2009; Sokolov & Rintoul 2009), creating a highly dynamic region with strong physical gradients. In the foraging area of king penguins to the south-east of Kerguelen, the juxtaposition of cold FTC waters of southern origin with PF waters as well as bathymetric-related effects, such as upwellings and the cold-water flow along the Kerguelen shelf break, may lead to a highly diverse and structured environment. Such diversity and

structuring in the ocean habitat may impact upon the distribution and biomass of many species, ranging from planktonic organisms to higher trophic levels such as myctophid fish (Gon & Heemstra 1990; Collins et al. 2008), and therefore to distinct and predictable prey field patterns in the foraging area used by king penguins. Furthermore the influx of cold southerly waters may represent an important input of nutrients and oxygen-rich waters into the foraging area of king penguins (Charrassin et al. 2002), enhancing biological productivity and increasing prey availability (Blain et al. 2007).

Variability in the FTC influx into the area to the south-east of Kerguelen appears to be closely related to the position of the PF to the north of the Chun Spur, presumably due to the direct juxtaposition of the two features with their contrasting physical properties and flow directions. However, the complex bathymetry of the Kerguelen Plateau leads to non-linear responses in these oceanographic features under differing environmental conditions, with abrupt changes in oceanographic patterns after a given environmental threshold is passed. Our work shows how the relationship between the relative positions of the FTC and the PF is variable with shifts from quasi-linear to non-linear behaviour, and with abrupt southward shifts of the FTC to the south of the Chun Spur when the PF is at 51.4°S or further to the south. These anomalous southward shifts of the FTC may indicate critical changes in the oceanographic habitat to the north of the Chun Spur, as the absence of the FTC influx may significantly affect biological productivity and oceanographic structures, and therefore the abundance and distribution of king penguins' prey. The co-variability of the FTC and the PF position suggest the PF position might be a suitable indicator characterizing the oceanographic habitat to the south-east of Kerguelen, taking into account the FTC influx over the Chun Spur as well as the southward extent of PF waters.

Changes in king penguins foraging behaviour and efficiency with the PF position indicate the importance of the FTC influx into the area to the south-east of Kerguelen for foraging

king penguins. Increased foraging trip duration of incubating birds, and reduced body mass gain of brooding birds suggests decreasing foraging efficiency with the PF moving southward, confirming the negative impact of PF southward shifts and reduced FTC influx on prey resources available to king penguins during both breeding stages. Such reduced foraging efficiency may result from lower catch per unit effort (CPUE) due to increased travel to more distant foraging locations, greater search or travel time between prey patches, or more frequent dive attempts to catch sufficient prey within a patch. Foraging habitat shifts away from slope areas during both breeding stages may indicate reduced profitability of prey resources associated with different features arising from the interaction of oceanography and bathymetry in shelf break areas such as upwellings and the cold-water tongue originating from the FTC influx. However, while brooding birds concentrated their foraging activity onto the Kerguelen Plateau, incubating birds moved into offshore and more southerly waters, where higher geostrophic velocities and SSH variance indicate the use of dynamic large-and mesoscale features such as ocean currents and eddies.

6.5.3 Behavioural responses of king penguins in relation to the breeding stage

The different responses of incubating and brooding birds to variability in environmental conditions and prey availability may reflect changes in priority with regard to offspring survival over the summer breeding season. Increased trip duration and BMG for incubating birds suggests that birds adapted their foraging behaviour to compensate for less favourable foraging conditions by longer at-sea times and exploration of offshore large-and mesoscale features. This may allow less colony-constrained birds during incubation to encounter more profitable and stable prey resources in exchange for longer foraging trips. During persistent anomalies, penguins increase their foraging range so far that they take the risk of breeding failure, being unable to return to their colony in time to relay the

partner (see Chapter 5). Such behaviour may reflect the life-history trade-off in long-lived seabirds, favouring adult survival over that of their offspring (Stearns 1992; Gauthier-Clerc et al. 2002; Groscolas et al. 2008); parents build up their own body reserves by taking the risk of breeding failure. The constant trip duration and decreased BMG of brooding birds indicates a higher priority for regular provisioning of chicks, hence ensuring chick survival while losing their own body reserves. This may indicate that birds have committed a certain level of resource to their offspring by the time brood starts, and they are prepared to take greater risks. Shifts in foraging areas onto the Kerguelen Plateau shelf may allow them to keep trip durations sufficiently short to ensure chick provisioning, but may also allow them to explore for any prey resources associated with small-scale oceanographic features (Park et al. 2008b; see Chapter 4). These features may be less profitable and stable than those associated with other features related to the FTC influx in proximity to the shelf break, or larger-scale oceanographic features in offshore areas at greater distances. Alternatively, penguins may switch their myctophid diet to a larger prey spectrum including squid and ice fish (C.A.Bost, pers.comm.).

The most significant behavioural changes occurred at the highest probabilities of FTC shifts, reflecting the significant effect of the absence of FTC water mass on oceanography and prey resources in the area to the south-east of Kerguelen, and may indicate points of critical change in foraging conditions for king penguins. In particular, diving behaviour and the vertical foraging habitat utilised by incubating birds showed changes with the FTC southward shifts, indicating important changes in prey resources in the upper ocean layers such as occur at the SML, TH and WW, which are known to be used by foraging king penguins (Charrassin & Bost 2002; Scheffer et al. 2012; see Chapter 4). The reduced presence of cold FTC water masses, and warmer PF waters approaching the Chun Spur presumably lead to changes in the thermal structure of the upper water column and associated prey resources used by king penguins. In case of such changes in the upper

ocean, CDW may provide an alternative foraging niche for diving predators, allowing adjustments of vertical foraging habitat to environmental variability and significant changes in upper ocean conditions and prey resources. As CDW is usually found at greater depths than the SML, TH and WW, it may be less affected by direct environmental forcing of ocean-atmosphere interactions (Roquet et al. 2009), which may lead to higher stability of associated prey resources (see Chapter 5). However, the possibility of such vertical foraging habitat adjustments by use of the CDW may be restricted to areas at greater distances from the colony in southerly offshore waters or over the southern part of the Northern Kerguelen Plateau, where CDW may be available within the diving range of king penguins at depths < 350m (Park et al. 2008b; Roquet et al. 2009; van Wijk et al. 2010). Due to these geographical restrictions, only incubating birds may be able to make such vertical foraging habitat adjustments. However, reduced wiggle numbers of incubating birds with FTC shifts indicate reduced foraging efficiency despite the horizontal and vertical foraging habitat changes, suggesting that the best foraging conditions are usually associated with features arising from the interaction of oceanography, presumably the FTC influx, with bathymetry in proximity to the Kerguelen Plateau shelf break.

The position of the PF and FTC in the area to the south-east of Kerguelen appear to be of key importance for the ocean habitat structure and the foraging of king penguins in terms of their surface travel and diving behaviour. Such significant impacts from changes in thermal structure confirms the importance of SST for foraging king penguins at Kerguelen as in other breeding localities (Bost et al. 2011). Our study suggests that critical changes in the oceanographic structure and associated prey resources of the foraging habitat of king penguins may occur when the PF changes position to south of 51.4°S in the area to the north of the Chun Spur, leading to possible southward shifts of the FTC.

6.5.4 Consequences of long-term climate change

With the projected southward shifts of the PF with climate change (Solomon et al. 2007) the PF may increasingly approach the Chun Spur, which may lead to reduced FTC influx over the Chun Spur. This may have important impacts on the oceanographic habitat in the area to the south-east of Kerguelen, potentially also significantly affecting king penguin foraging. However, as oceanographic and oceanographic-bathymetry interactions at the Chun Spur are complex, these hypotheses must remain somewhat speculative and limited to patterns observed during our study period.

6.5.5 Interest of diving predators to behavioural studies

Our study shows the impact of environmental variability, particularly in the positions of the PF and FTC, on king penguins breeding at Kerguelen both in terms of surface and diving behaviour. King penguins breeding at Crozet have already been shown to be impacted by changes in the PF position (Péron et al. 2012) and SST (Le Bohec et al. 2008). Our study confirms this hypothesis for king penguins breeding at Kerguelen. However, bathymetry-oceanography interactions at Kerguelen appear to induce non-linear responses in other important oceanographic features and associated prey resources, potentially leading to drastic changes in king penguins foraging behaviour.

Studies of the impact of climate change on king penguins breeding at Crozet were based on survival rates (Le Bohec et al. 2008), but future studies may need to take into account other important factors affecting king penguins' population growth (Barbraud et al. 2008). Studies based on surface behaviour only (Péron et al. 2012) do not take into account changes in the vertical habitat and diving behaviour of penguins, which play crucial roles for understanding animals' behaviour towards environmental variability. In this study, the

combination of behaviour and habitat descriptors in the horizontal and vertical dimension allowed us to gain more detailed insights into a diving predators' behavioural responses in relation to oceanographic conditions at the ocean surface and at depth. Thus, this approach allowed us to find possible explanations for changes in the animals' foraging behaviour associated with environmental change. The thermal structure of the water column has been shown to play a key role for diving predators (Brill et al. 1993; Brill & Lutcavage 2001; Cartamil & Lowe 2004; Scott & Chivers 2009) and king penguins in particular (Charrassin & Bost 2001; Scheffer et al. 2012). Significant changes in diving behaviour and vertical foraging habitat use by king penguins breeding at Kerguelen underline the importance of oceanographic conditions at depth for birds and environmental variability. By taking into account the variability in the vertical foraging habitat and behavioural adaptations of animals, future studies should develop a more comprehensive understanding of the reactions of diving predators towards environmental change.

King penguin populations have increased since the 1960's (Delord et al. 2004; Bost et al. 2012) despite warming of the Southern Ocean (Solomon et al. 2007). Our study shows that king penguins can adjust their behaviour to environmental conditions encountered, presumably enabling them to buffer reproductive success and population survival against environmental variability. However, it appears that such adaptive capacities can buffer changes in environmental conditions only to a certain extent and that threshold conditions may exist, limiting an animals' capacity to buffer reductions in prey availability by adaptations in foraging behaviour (Piatt & Sydeman 2007; Harding et al. 2007; Ronconi & Burger 2008). This effect may be enhanced by non-linear responses in oceanographic conditions and prey availability to changes in environmental conditions, as appears to be the case in the area to the south-east of Kerguelen.

Chapter 7

General Discussion



This thesis explores the foraging behaviour of breeding king penguins in a spatially and temporally variable environment. As a biological model king penguins exhibit potentially noticeable advantages. First, it is a long-distance forager and deep diver with major constraints as a flightless bird and a central place forager (Weimerskirch 2007). The field work was based on the analysis of behavioural and environmental data (sea water temperature) from tagged penguins foraging in two of the main breeding locations of the Southern ocean: South Georgia (South Atlantic) and Kerguelen Islands (South Indian). Studying king penguins in two different sectors of the Southern Ocean facilitated the analysis of the penguins foraging behaviour under different physical conditions, providing insights into key oceanographic features and potential behavioural adaptations under differing environmental conditions and energetic constraints.

For both breeding locations we identified the key oceanographic features targeted during foraging in both the horizontal and vertical dimension, and king penguin behavioural patterns as they explore these features. This allowed, as a first step, an investigation into penguin foraging behaviour in relation to the oceanographic habitat of the different breeding locations. Combining both datasets in a comparative study further enabled me to identify common patterns in how penguins explore their oceanographic habitat as well as any behavioural differences resulting from any local habitat characteristics. This provides insights into potential key features of king penguins foraging as well as behavioural patterns allowing the efficient exploration of environmental features under different conditions and different constraints on the animals. From this, I attempted to gain insights into behavioural adaptations of king penguins to environmental variability as well as into potential reactions towards changes in the environment and to key specific oceanographic features.

7.1 Foraging between the Polar Front and the SACCF

With breeding colonies situated south of the PF, king penguins at both study locations explored the area between the Polar Front (PF) and the southern ACC Front (SACCF). Birds at different breeding stages showed distinct patterns exploring different oceanographic features in terms of foraging areas and thermal features at depth. Foraging trips of incubating birds extended to the PF during early summer (December-January), and shifted to the SPF during late summer (February). Brooding birds foraged in areas close to the colony, where they explored cold-water features of southern origin, the SACCF at South Georgia and the cold-water subsurface current originating from the Fawn Trough Current (FTC) at Kerguelen. Such changes in foraging trip characteristics of central-place foragers at different times of the summer season are known to occur and are thought to be the result of changing time constraints arising from the need to supply their offspring with food. Increasing time pressure may lead to a shortening of foraging trips with the advancing summer season as reported for other penguin species (Bost et al. 1997; Charrassin et al. 1999; Charrassin & Bost 2002; Lescroel & Bost 2005). However, the consistency of foraging patterns in relation to oceanography observed at both study locations despite differences in local habitat and the detailed location of the islands in relation to the PF suggests that such behaviour may represent general patterns of foraging behaviour and adaptations to oceanography. However, prey behaviour may also play important roles, but remains mostly speculative due to lack of information and data.

7.1.1 Foraging at the Polar Front and south Polar Front

Importance of the PF according to the breeding location and season

Foraging trips of incubating king penguins breeding at South Georgia and Kerguelen were directed towards PF waters, confirming the importance of the PF as a foraging area for king penguins breeding at South Georgia and Kerguelen. The PF is known to be a key

foraging area for marine predators of the Southern Ocean (see review Bost et al. 2009) due to the occurrence of prey resources at high densities and shallow depths (Kozlov et al. 1991; Collins et al. 2012), therefore providing favourable foraging conditions for diving marine predators such as king penguins. However, foraging trips of king penguins extended into the PF only during early summer, and shifted towards the southern PF boundary during late summer (see Fig. 4.1 Chapter 4; Fig. 3.3 Chapter 3). While the change in foraging areas to the southern PF corresponds to a shortening of foraging trips at South Georgia and therefore to behavioural patterns expected with the advancing summer season, king penguins at Kerguelen increased their foraging distances when foraging in the southern PF parts during late summer (see Table 5.1). Such common patterns in the exploration of the different PF areas, despite differences in habitat accessibility, may indicate different prey patterns in terms of availability and energetic value associated with the PF core and its southern boundary, with the southern boundary appearing to be a more suitable foraging habitat than the PF core during late summer at both breeding locations. Similar patterns in diving behaviour of birds exploring the different PF zones further suggest such differences in prey distribution, with the PF allowing for foraging at shallower depths (Fig. 7.1). Common behavioural patterns at South Georgia and Kerguelen suggest that such differences in prey distribution as well as their exploration by foraging king penguins during different times of the summer season may be similar at both breeding sites. During the extended incubation trips, the penguins are able to forage at more distant locations and have access to a potentially more profitable area. During incubation, prey distribution resulting from the oceanographic structure of the foraging habitat thus appeared to play a more important role than spatial constraints in the adjustment of foraging strategy in king penguins.

	Early Inc	Late Inc	Brooding	Reference
South Georgia	556 ± 32	462 ± 25	222 ± 25	
Kerguelen	470 ± 48	263 ± 12	263 ± 12	
Crozet	448 ± 40		228 ± 29	Charrassin & Bost 2001
	394 ± 33		351 ± 21	Bost et al. 1997
	336 ± 105		324 ± 155	Jouventin et al. 1997

Table 7.1: Maximum distances from the colonies reached by foraging king penguins during early incubation, late incubation and brooding.

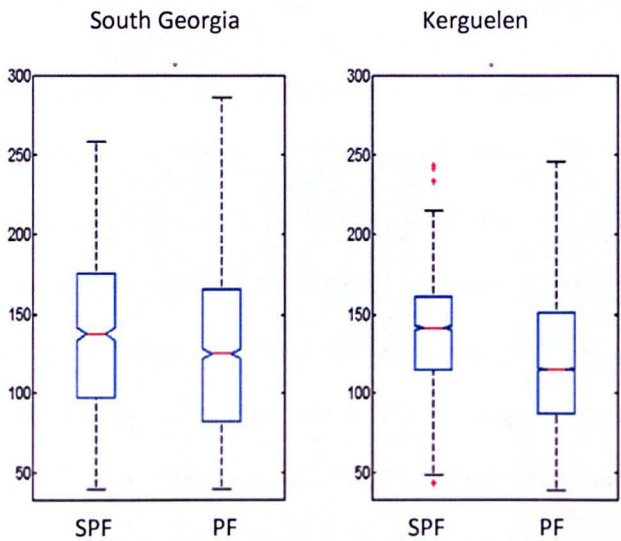


Figure 7.1: Bottom start depths of king penguins foraging in the PF and at the southern PF edge (SPF).

Frontal zones are characterized by different properties in terms of hydrological structure and oceanographic dynamics (Orsi et al. 1995; Park et al. 2008b; Venables et al. 2012), which may lead to distinct patterns of prey resources that associate with such features (Pakhomov et al. 1996). The PF is characterized by strong thermal gradients from the juxtaposition of the different water masses, leading to dense prey aggregations at shallow depths (Kozlov et al. 1991; Collins et al. 2008; Collins et al. 2012). However, strong

velocities and vertical mixing associated with frontal cores may lead to increased spatial and temporal variability in hydrological structures and associated prey resources (Spear et al. 2001). The exploration of such highly profitable prey resources at the PF may therefore be associated with increased search times between prey patches due to the high spatial variability and dispersion of prey patches. The potentially high time investment needed to search for prey patches may decrease the suitability of the PF when birds are under increasing constraints with the advancing summer season, making prey resources of higher stability associated with areas other than the PF core more important.

Potential role of frontal boundaries for profitable foraging

Characterized by lower levels of mixing and lower velocities compared with frontal cores, frontal boundaries may provide for more stable hydrological structures and therefore higher stability in associated prey resources (Spear et al. 2001), which may provide for more suitable foraging conditions during periods of increased constraints in the late summer season. Foraging patterns of king penguins at Kerguelen underline such suggestions when compared with South Georgia, as habitat suitability of the southern PF boundary at South Georgia may be biased by shorter distances to the colony. Foraging at the southern PF by king penguins breeding at Crozet (Charrassin & Bost 2002; Péron et al. 2012, see Fig. 7.2) may further underline the importance of the southern PF boundary as a foraging area for king penguins. In contrast to South Georgia and Kerguelen, Crozet is located to the north of the PF, and foraging in southern parts of the PF despite being the most remote PF area from the colony may underline the penguins' preference of this area to the PF core and its northern boundary, as well as to the Subtropical Front (STF) to the north of Crozet. Both PF boundaries are characterized by lower velocities and vertical mixing than the PF core, and may therefore provide for prey resources of higher stability. A decreasing Winter Water (WW) depth in southern areas of the PF compared with its

northern boundary, together with the presence of the still relatively warm Surface Mixed Layer (SML) waters $>4^{\circ}\text{C}$ of the PF (Park et al. 1993) may lead to the occurrence of strong

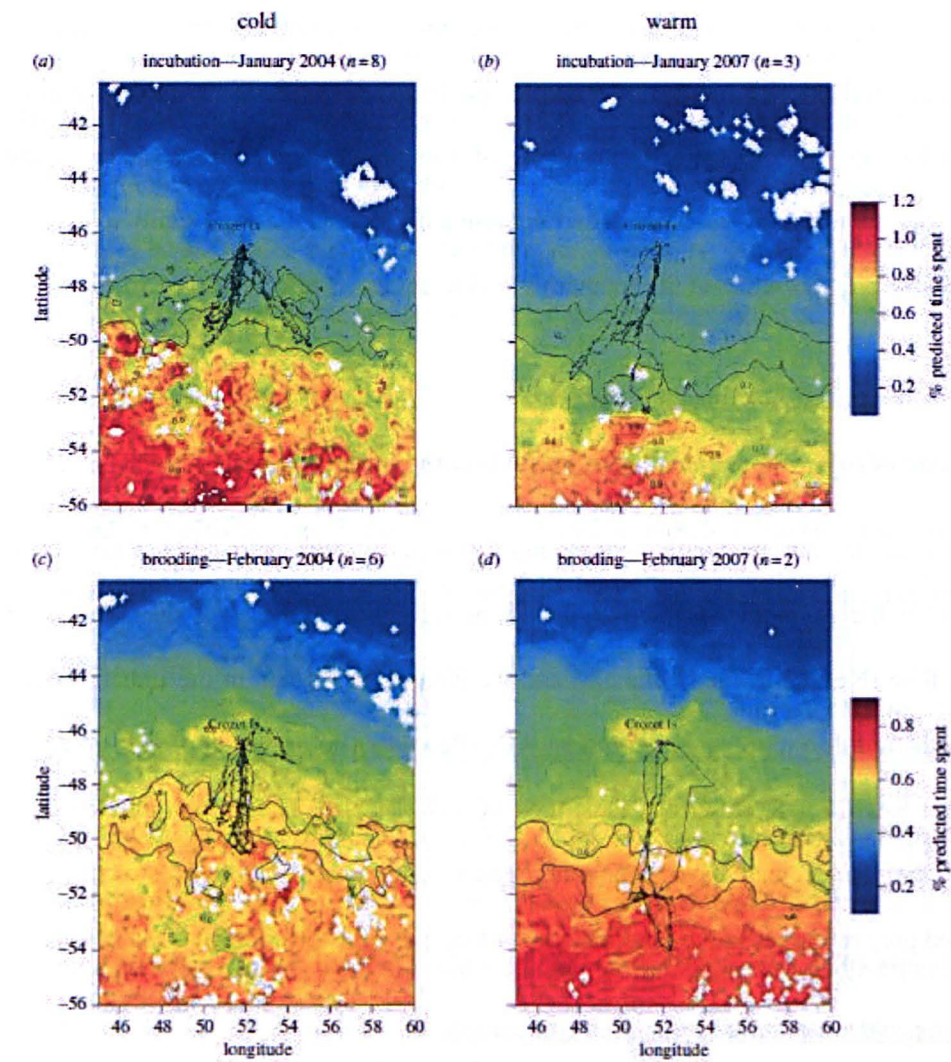


Figure 7.2: Foraging trips of king penguins breeding at Crozet (medium black lines with dots) on their predicted spatial distribution from habitat modelling, showing the exploration of the PF and SPF. Thick black lines correspond to 4°C and 5°C isotherms indicating the PF. Figure from Peron et al. (2012).

thermal gradients at relatively shallow depths, which may offer more profitable foraging conditions for king penguins than the northern boundary.

Role of the geographic location of the breeding colony: breeding to the south of the PF

The location of the colony in relation to the PF may therefore play an important role in the foraging strategy of king penguins in terms of possible behavioural adaptation to changing breeding constraints. At South Georgia and Kerguelen, better accessibility to the southern PF boundary may allow better adjustments of foraging behaviour in relation to the animals' constraints, allowing birds under increasing constraints the opportunity to explore more suitable prey resources at the southern PF with less travel effort than at Crozet.

7.1.2 Influx of cold waters of southern origin into the foraging area

The oceanography around South Georgia and Kerguelen is characterized by a northward deviation of the southern ACC flows by the prominent bathymetry of the North East Georgia Rise (NEGR) in the Scotia Sea and the Kerguelen Plateau in the Indian Ocean. Such northward deviations of the southern ACC flow leads to an influx of cold southern waters, the SACCF at South Georgia and the FTC at Kerguelen. These flows into the areas close to the islands may have important impacts on the oceanographic structure and associated prey resources in the foraging area of king penguins breeding at these islands.

Role of the cold-water influx for marine productivity

The influx of the cold waters of southern origin leads to enhanced nutrient input into the areas close to the breeding colonies, resulting in increased phyto-and zooplankton development (Thorpe et al. 2002b; Ward et al. 2002; Thorpe et al. 2004; Murphy et al. 2007), certainly also affecting the abundance of myctophids preying upon the zooplankton (Shreeve et al. 2009). The ecological importance of waters associated with the southern ACC fronts (SACCF, SB) has already been suggested for primary productivity and baleen whale abundance at a circumpolar scale (Tynan 1997; Tynan 1998) as well as for nutrient

enrichment and increased phyto-and zooplankton development in the Scotia Sea (Thorpe et al. 2002b; Ward et al. 2002; Thorpe et al. 2004; Murphy et al. 2007). At Kerguelen, the cold-water tongue originating from the FTC has been suggested to play a key role for providing iron-input to the Kerguelen Plateau ecosystem (Charrassin et al. 2002), which plays a critical role for primary production on the Kerguelen Plateau. In both locations, brooding king penguins exploring the cold-water influx indicate profitable myctophid resources to be associated with these water masses, suggesting the importance of this cold-water influx for king penguins and potentially other marine predators.

The approach of the cold-water influx with the warmer PF waters may furthermore lead to increased thermal gradients at the southern edge of the PF, which may further enhance biological productivity and biomass accumulation and therefore increase the profitability of prey resources at the southern PF edge and adjacent areas for king penguins and potentially other marine predators.

Role of the ACC flows in ecosystem structuring and foraging niches of marine predators

The northward deviation of the southern ACC flows and their close juxtaposition with PF waters furthermore leads to the presence of several distinct ACC features in a spatially restricted area in proximity to the breeding colonies at South Georgia and Kerguelen. This may lead to a highly segregated and diverse environment, providing for the presence of several distinct foraging niches in the area explored by foraging king penguins. Such habitat characteristics may allow higher behavioural diversity and distinct behaviour during the foraging trips and lead to better adjustments of foraging strategy to breeding constraints, which may ultimately result in increased foraging profitability over the summer breeding season. This may drive individual fitness, as niche variation among individuals is thought to be a major source of variation in fitness (Svanback & Bolnick 2005). Furthermore habitat segregation and niche separation may decrease inter-and

intraspecific competition (Pianka 1981; Svanback & Bolnick 2005), which may be particularly important during periods of increased constraint and competition for resources such as during chick raising in summer. Similar mechanisms have been suggested for sexual habitat segregation in grey seals (Breed et al. 2006) and age-based habitat segregation in southern elephant seals (Field et al. 2005). The high degree of horizontal and vertical habitat segregation may allow king penguins to efficiently exploit resources in agreement with the theory proposed for age-based niche segregation (Polis 1984). The impact of environmental variability may also be buffered, as alternative foraging locations and niches may be targeted if others become unavailable or less profitable. The presence of a segregated and diverse environment, particularly the presence of alternative foraging locations in close proximity to the colony, may therefore represent important elements in the birds foraging strategy, especially when under increased constraints.

Advantages of Kerguelen and South Georgia with respect to energetic requirements

So far such strong habitat segregation and the presence of alternative foraging niches have not been reported for king penguins from other locations. Concerning other penguin species, a large foraging plasticity have been described among inshore feeders such as Gentoo penguins *Pygoscelis papua* (Lescroël & Bost 2005). Patterns described from Crozet suggest changes in foraging characteristics of king penguins over the summer season mainly in terms of dive depth and foraging range at the end of summer. However, the lack of accessible foraging niches in proximity to the colony appears to allow less behavioural adaptation to increasing breeding constraints in terms of reduction of foraging trip duration and increases in profitability. The segregated environment and the presence of several distinct foraging niches in the foraging areas of king penguins breeding at South Georgia and Kerguelen appear to provide for favourable conditions for adaptation of foraging strategy to breeding constraints. At both of our study locations, brooding king

penguins foraged in the area to the south of the PF at closer distances to the colony, where they explored features below the thermocline related to the cold-water influx of southern waters, Circumpolar Deep Water (CDW) in the SACCF influx at South Georgia, and WW in the cold-water subsurface tongue from the FTC at Kerguelen. Such alternative foraging niches in proximity of the colony allow king penguins breeding at South Georgia and Kerguelen to explore prey resources at short distances from the colony during brooding, keeping trip distances much shorter than at Crozet where the northern PF boundary appears to provide for the closest foraging grounds for king penguins of all breeding stages. The lower travel costs for king penguins breeding at South Georgia and Kerguelen during the brooding stage may result in higher foraging efficiency, which may be of particular importance with increasing constraints on the animals. Additionally the expression of two distinct patterns of foraging behaviour shown by brooding birds at South Georgia (Brooding I – Brooding II, see Chapter 3) may indicate that the oceanographic environment and prey distribution in the area to the north of South Georgia may allow higher flexibility and adjustment of foraging strategies. It may be valuable to examine king penguin foraging behaviour elsewhere in order to determine if this is also evident; similarly, it would be valuable to sample birds from South Georgia in other seasons, to see if this is a permanent behavioural trait.

Potential role of high stability in the cold-water flows in the Scotia Sea and to the east of the Kerguelen shelf

The highly constrained nature of the cold-water flows in the Scotia Sea and to the east of the Kerguelen Plateau may lead to a high level of stability for the habitat characteristics resulting from the cold-water influx. In the area to the north of South Georgia, the SACCF shows a lower monthly spatial variability compared with areas further south as well as when compared with the PFZ (Boehme et al. 2008). This is possibly because the flow is constrained by bathymetry. At Kerguelen, the cold-water subsurface tongue originating from the FTC is channelled along the eastern shelf break of the Kerguelen Plateau, leading to high spatial stability of this flow (Park et al. 2008b; Roquet et al. 2009). The particular conditions of the Scotia Sea and the Kerguelen Plateau may therefore make the cold-water influx from the SACCF and FTC and resulting oceanographic features predictable habitat characteristics, which may increase the profitability of feeding success in these foraging areas for king penguins and potentially other marine predators.

In addition to the location to the south of the PF, with better access to prey resources at the SPF, the northward deviation of cold southern waters and their juxtaposition with the PF may provide for favourable foraging conditions for king penguins breeding at South Georgia and Kerguelen through increased nutrient input, the sharpening and stabilizing of frontal signatures as well as increasing habitat segregation, which may all be factors increasing foraging habitat suitability and profitability for marine predators such as king penguins.

Comparison with foraging patterns of other southern king penguin populations

The exploration of oceanographic features in the area to the south of the PF may be a common feature of king penguins breeding south of the PF. King penguins from Heard Island show similar foraging zones to those breeding at Kerguelen, exploring areas to the

east and south-east of Kerguelen as well as areas coinciding with the FTC flow over the Chun Spur (Moore et al. 1999a; Wienecke & Robertson 2006; van Wijk et al. 2010; Hindell et al. 2011). Although there is no detailed information about their use of frontal zones and spatio-temporal variability in foraging patterns with circulation patterns over the Chun Spur, foraging behaviour reported for king penguins breeding at Heard Island suggests they explore oceanographic patterns similar to those at South Georgia and Kerguelen.

The potential importance of such cold-water influx into the foraging area and its meeting with PF waters is underlined by the breeding season 2009/10 at Kerguelen, where the reduced cold-water influx from the FTC over the Chun Spur into the foraging area resulted in significant changes in foraging behaviour and reduced breeding success of king penguins. At South Georgia, the oceanographic warm anomaly in the area to the north of South Georgia may also have impacted the cold-water influx from the SACCF. However, as there are no details on oceanographic patterns or foraging behaviour of marine predators during that season, this statement remains speculative.

7.1.3 Circumpolar Deep Water (CDW) use by foraging king penguins

At both study locations, king penguins appeared to explore prey resources associated with CDW and modified CDW (mCDW). King penguins are known to explore the water column in a directed way and to target specific depth levels in relation to the hydrothermal structure (Charrassin et al. 1999; Charrassin & Bost 2001; Charrassin et al. 2004; Trathan et al. 2008; Scheffer et al. 2010), presumably targeting most profitable and accessible prey resources associated with specific thermal features or water masses. The thermocline and WW have been identified as representing important features for foraging king penguins (Charrassin & Bost 2002). Until now, king penguins have not been reported as exploring

water masses below WW such as CDW. In our study, however, bottom periods directed into CDW indicate they do target profitable prey resources associated with CDW at both South Georgia and Kerguelen. Such behaviour in both study locations suggests CDW represents an important and consistent feature in the foraging habitat of king penguins in addition to the upper ocean water masses such as the TH and WW, at least when foraging in southern parts of the PF.

CDW is characterized by high levels of nutrients and Fe, stimulating biological productivity through the input of nutrients into the upper water column (Prezelin et al. 2000; Klinck et al. 2004; Moffat et al. 2009; Dinniman et al. 2011). Particularly mCDW formed at the upper CDW boundary through mixing with WW, is thought to play a key role for such nutrient enrichment and biological activity (see Dinniman et al. 2011). The discontinuity in physical properties between WW and CDW may furthermore act as a barrier for sinking matter as well as for primary and secondary production, enhancing biological activity and biomass accumulation (Hofmann & Klinck 1998) at the boundary between WW and CDW as suggested for the thermocline (TH) (Charrassin & Bost 2002) and the Sub-Antarctic Mode Water (SAMW) limit in the context of elephant seal foraging (Muelbert et al. 2012). Such a layer of high nutrient content and potential biomass accumulation characterized by distinct physical properties may attract zooplankton, which is in turn consumed by mid-trophic levels such as myctophids (Shreeve et al. 2009). The upper CDW boundary and mCDW may therefore host potentially profitable prey resources for diving marine predators. Significant increases in myctophid density and/or species diversity (Pusch et al. 2003; Donnelly & Torres 2008) and the occurrence of species consumed by king penguins (Collins et al. 2012) at the transition between WW and CDW at depths of 200-400m may indicate prey resources of high profitability associated with the start of CDW in the water column. This is further supported by the observation of highest myctophid biomasses at depths of 200 - 400 m in the Scotia Sea (Collins et al. 2008). Such

myctophid aggregations of high density and potentially different energy content may represent profitable prey resources for diving predators such as king penguins.

Dive depth is one of the most important factors in foraging adjustment for air-breathing marine predators (Boyd 1997; Mori & Boyd 2004; Green et al. 2005), and if prey are deep, dive depth will restrict the access of king penguins to potential prey resources associated with CDW. While larger marine predators with higher breath-hold capacities, such as elephant seals, are known to explore myctophids in deeper water masses such as CDW (Cherel et al. 2008; Costa et al. 2008; Costa et al. 2010; Biuw et al. 2010), these prey resources may be inaccessible to smaller species of lesser breath-hold capacity, such as king penguins. However, upwellings may lead to CDW intrusions into the upper water column (Prezelin et al. 2000; Klinck et al. 2004; Moffat et al. 2009), resulting in the occurrence of CDW at shallower depths accessible to king penguins. The strong vertical mixing and input of nutrient-rich CDW into the upper water column may enhance biological productivity (Prezelin et al. 2000; Klinck et al. 2004; Moffat et al. 2009; Dinniman et al. 2011) and further attract higher trophic levels in such upwelling locations, as indicated by increased abundance and body sizes of Antarctic krill associated with CDW intrusions at the West Antarctic Peninsula (WAP) (Lawson et al. 2004). CDW upwellings may lead to the occurrence of profitable myctophid aggregations at relatively shallow depths, and represent attractive foraging habitats for marine predators such as king penguins. CDW intrusions onto shelf areas have been reported as attractive to foraging elephant seals in the WAP area (Costa et al. 2008; Costa et al. 2010), at the northern Antarctic Peninsula (Muelbert et al. 2012) and in the Weddel Sea (Biuw et al. 2010), and have also been suggested as playing an important role for the winter foraging of Adélie penguins breeding at the WAP (Erdmann et al. 2011). Our study suggests that king penguins at South Georgia and Kerguelen may exhibit similar behaviour when they target CDW at both study locations.

Interactions of the southern ACC flow with pronounced bathymetric features appears to provide for conditions favouring such CDW intrusions into the upper water column, as reported for the SACCF and SB approaching the Antarctic continental shelf at the WAP (Klinck et al. 2004; Moffat et al. 2009) and at other locations around Antarctica (Prezelin et al. 2000). At South Georgia and Kerguelen, the SACCF and FTC flows approaching the Kerguelen Plateau and South Georgia shelf may provide for similar conditions for such bathymetry-related CDW upwellings leading to local CDW intrusions into the upper water column. The spatial coincidence of CDW bottom periods with those of the SACCF and FTC flows in proximity of the South Georgia and Kerguelen shelf break (see Fig. 7.3) indicates that CDW intrusions explored by foraging king penguins may result from the interaction of southern ACC flows with any particularly pronounced bathymetry.

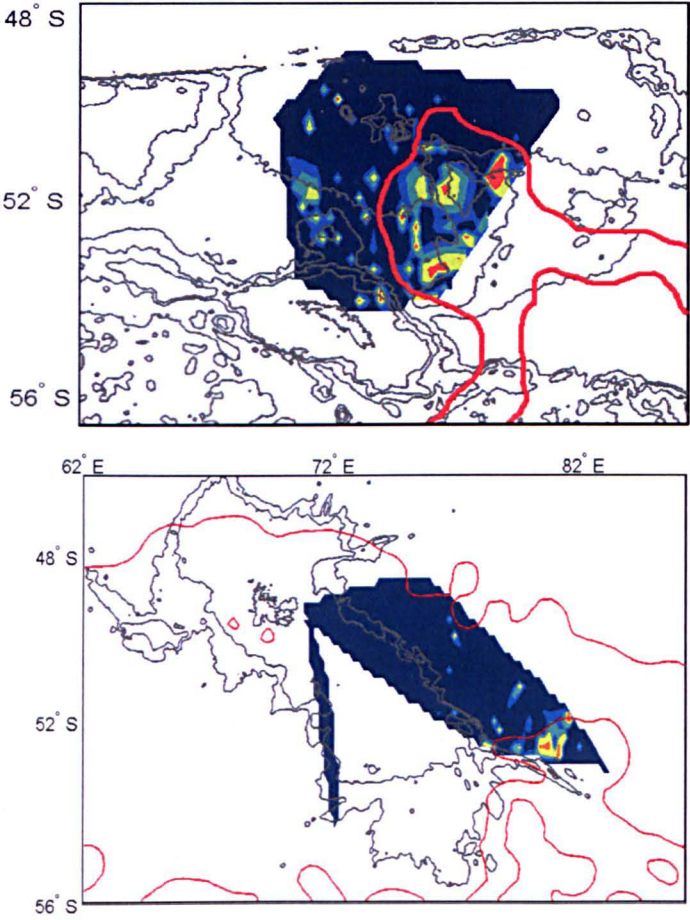


Figure 7.3: Spatial patterns of CDW exploration, indicated by relative bottom time of king penguins spent in CDW, and ACC frontal positions (indicated in red, based on SSH signatures following Venables et al. 2012) at South Georgia and Kerguelen. According to our results of CDW use during the different breeding stages at our study sites CDW use for South Georgia includes incubating and brooding birds, for Kerguelen only incubating birds.

CDW occurrence at Kerguelen

CDW occurrence at shallower depths of <250 m (i.e. at depths accessible to king penguins) in proximity of the eastern Kerguelen Plateau shelf break (van Wijk et al. 2010) as well as the presence of CDW and cold WW of southern origin at parts of the Kerguelen Plateau shelf (Park et al. 2008b) may indicate the upwelling of southern water masses at the Kerguelen Plateau. The pronounced troughs and canyons of the Kerguelen Plateau may also play an important role in defining such upwelling areas similar to the Marguerite Trough at the WAP, as suggested for the Heard McDonald Islands (HMI) Trough for the influx of CDW and cold WW from the FTC onto the Kerguelen Plateau (Park et al. 2008b). CDW exploration by king penguins mainly occurred in a restricted area to the north of the Chun Spur corresponding to CDW patterns from the FTC flow over the Chun Spur (Roquet et al. 2010), where upwelling of the CDW flow at the Chun Spur bathymetry may occur.

CDW occurrence at South Georgia

At South Georgia, spatial patterns of CDW exploration by king penguins generally coincided with the path of the SACCF influx and its reflection to the north of South Georgia (Thorpe et al. 2002b; Thorpe et al. 2004; Boehme et al. 2008). High nutrient content and krill biomass as well as a change in CDW properties at the SACCF (Ward et al. 2002; Ward et al. 2012) may further increase the habitat suitability of CDW associated with the SACCF influx for myctophids. Isopycnal doming at the SACCF fluxes in the area to the north of South Georgia (Ward et al. 2002), appears to lead to the presence of CDW at depths <250 m (Brandon et al. 1999; Thorpe et al. 2002b; Ward et al. 2002; Ward et al. 2012), and may result in the occurrence of profitable prey resources associated with CDW at accessible depths for foraging king penguins. Even though processes associated with CDW flooding the shelf at South Georgia and Kerguelen have not been described in detail,

our study suggests that similar oceanographic patterns occur and CDW upwelling may be of ecological importance to marine predators such as king penguins.

Profitability of CDW

High levels of dive effort and decreasing foraging performances in terms of available bottom time suggest high energy costs are associated with CDW exploration at both South Georgia and Kerguelen. However, CDW and modified CDW (mCDW) at the boundary with the overlaying WW may represent a distinct environmental niche in terms of physical and biogeochemical properties of the water column, which may host distinct myctophid resources of potentially increased profitability compared to those in the upper water column (Pusch et al. 2003; Collins et al. 2008; Collins et al. 2012). If prey in deeper water masses are easier to capture or are of higher energetic value, then deeper foraging strategies can be more efficient than shallow dives (Zimmer et al. 2010). At South Georgia, brooding king penguins consistently targeting CDW while foraging close to the colony, suggests that they do explore such profitable prey resources associated with CDW. The potential profitability of CDW prey resources, at least at South Georgia, may be indicated by the high body mass gains of Brooding II birds foraging in CDW compared to Brooding I birds exploring shallower TH prey resources, as suggested in Scheffer et al. (2012). Reduced Broadness Index (BrIdx) and wiggle numbers with high body mass gains of Brooding II birds suggests increased foraging efficiency in these deep waters, with higher energy return per distances travelled, bottom time and number of wiggles invested for prey capture. Such high foraging efficiency may be related to higher catch rates (e.g. patch size or density), or the prey targeted may be of different energy content (e.g. of different size or body composition) when exploring CDW.

Generalization: use of deep high-energy prey by diving predators

The exploration of deep high-energy prey associated with a change in hunting technique has been reported for pilot whales (Aguilar Soto et al. 2008), and may correspond to the observed higher foraging efficiency with changes in bottom behaviour of king penguins exploring CDW. Targeting more profitable prey resources at greater depths has also been reported from other marine predators such as baleen whales (Panigada et al. 1999) and swordfish (Chancollon et al. 2006) as well as for emperor penguins (Klages 1989), and has been proposed to indicate different foraging modes for sperm whales (Teloni et al. 2008). Foraging mode is thought to integrate a range of traits such as habitat preference, prey, energy budget and reproductive effort (Huey & Pianka 1981), and can be used to determine whether predators switch foraging tactics (Laughlin 1989). So far, such analyses have mostly been carried out for predators where prey capture behaviour can be directly observed. However the separation of different patterns based on foraging characteristics and targeted environmental niches with potentially different prey may suggest the presence of different foraging modes for king penguins when exploring prey resources associated with CDW opposed to the TH and WW. Despite the occurrence of mixed patterns due to the continuous variation in foraging activity (Cooper 2005), two main patterns of behaviour and targeted foraging niches emerged for brooding birds at South Georgia, long bottom periods and high wiggle numbers targeting shallow waters near strong vertical temperature gradients, and short bottom times with low wiggle numbers with apparently higher foraging efficiency into deep CDW and mCDW in areas closer to the colony. However, such clear behavioural patterns may be related to the presence of distinct environmental niches and associated prey resources at South Georgia. In different environments, the observed behaviour may result from variable degrees of expression of different foraging modes, which may be determined by the animals' constraints as well as oceanographic and prey conditions encountered.

Synthesis: CDW use at South Georgia

High energetic costs for diving and short proportions of time available for dive bottom periods which were associated with the exploration of deep waters suggests that king penguins may preferentially forage in the TH and WW, and target CDW only in cases where there was insufficient prey resources at shallower depths. The occurrence of CDW exploration may therefore depend on the animals' energy requirements associated with current breeding constraints, and on prey distribution related to seasonal effects or environmental variability.

CDW use at Kerguelen

At South Georgia, high time and energy constraints during brooding and potential seasonal depletion of prey resources in the area close to shore may be the reason for the costly exploration of CDW while minimizing travel effort and maximizing foraging efficiency. At Kerguelen, increased CDW exploration occurred under high pressures from environmental conditions impacting prey distribution in the TH and WW. In both locations, CDW exploration increased with increasing pressure on the penguins by seasonal or environmental constraints. CDW exploration may therefore be a strategy for coping with elevated pressures arising from breeding constraints, seasonal prey depletion effects or environmental variability, potentially allowing penguins to buffer insufficient prey resources in the TH and WW. However, CDW was also targeted by incubating birds at Kerguelen and South Georgia, indicating that such behaviour may not only occur when forced by high constraints. Deeper dives with CDW exploration towards the end of incubation foraging trips appears similar to behaviour reported from elephant seals at the Northern Antarctic Peninsula (Muelbert et al. 2012), suggesting that CDW prey resources may be targeted just before the animals' return to the colony. While such behaviour may

also be impacted by local oceanographic patterns, it may underline the potential profitability of prey resources associated with CDW to foraging marine predators.

CDW use at Crozet

CDW exploration by king penguins may be limited to areas to the south of the PF, where CDW may shoal to sufficiently shallow depths. In locations to the north of the PF, greater CDW depths may not allow the exploration of CDW prey resources, as indicated by temperature profiles recorded by foraging king penguins breeding at Crozet showing exclusively TH and WW exploration during their summer foraging trips (Charrassin & Bost 2002). However, during autumn when foraging trips extended further south, the exploration of warmer water masses below the T_{\min} WW layer (Charrassin & Bost 2001 Fig. 7) may indicate foraging on CDW prey resources. In breeding locations to the south of the PF, CDW exploration by king penguins may depend on local oceanography in terms of spatial patterns of CDW circulation and the presence of pronounced bathymetric features to create such upwellings. At South Georgia, CDW at accessible depths in proximity of the colony appears to allow highly profitable foraging, while such a CDW niche near the colony does not seem to exist at Kerguelen.

CDW use at Heard Island

At Heard Island situated to the south of Kerguelen, king penguins have been reported to generally forage in proximity of the shelf break to the south and the east of the island (Costa et al. 2011). In these locations, CDW upwellings of the FTC meeting the Kerguelen Plateau may occur at close distances from the breeding colony, which may result in accessible CDW prey resources in proximity to the colony, similar to South Georgia. However, due to the lack of information on thermal properties of the water column encountered by king penguins breeding at Heard Island, such suggestions remain speculative.

CDW: a stable and predictable foraging niche at greater depths

The CDW is not directly exposed to the atmosphere as are the water masses of the upper water column; therefore, CDW may be less impacted by atmospheric forcing (Roquet et al. 2009), therefore potentially representing a foraging niche of relatively high spatial and temporal stability. During the breeding season of 2009/10 at Kerguelen, atmospheric anomalies lead to changes in prey distribution in the TH and WW (see Chapter 5). However, prey resources associated with CDW may have been less impacted by the atmospheric anomaly, potentially providing for alternative prey resources. However, changes in upper-ocean conditions in 2009/10 appeared to be too drastic to be buffered by switching to CDW foraging, indicating the supplementary and not exclusive character of foraging on CDW prey resources at Kerguelen. At South Georgia, the CDW niche in proximity to the colony appears to provide for sufficiently profitable prey resources to represent a potentially exclusive foraging niche, at least for king penguins during brooding. Such differences may underline the importance of local oceanography in the breeding location for CDW foraging patterns and the profitability of such behaviour. However, while the coincidence of oceanography during our study years at South Georgia with general oceanographic patterns in the area to the north of South Georgia indicate that CDW exploration may be a constant foraging element under normal oceanographic conditions, it remains open whether and to what extent seasonal or interannual variability in oceanographic conditions may impact CDW flow patterns and associated prey resources in the area to the north of South Georgia.

CDW intrusions arising from ACC-bathymetry interactions may be impacted by wind events (Thoma et al. 2008), and have been suggested to be affected by changing wind fields around Antarctica in the context of climate change (Wallace et al. 2008). Such changes in CDW intrusions may imply changes in the foraging habitat of king penguins

and potentially other marine predators exploring associated prey resources. Being a potentially important foraging habitat for foraging king penguins, changes in CDW intrusions may ultimately impact the foraging behaviour and success of king penguins. However, such statements remain speculative, and to be confirmed require further studies on the behaviour and profitability of king penguins and other marine predators associated with CDW such as elephant seals (Costa et al. 2008; Costa et al. 2010; Muelbert et al. 2012) et Adélie penguins (Erdmann et al. 2011).

7.2 Different local habitats and implications for foraging behaviour and profitability

Role of local bathymetry

Despite similarities between locations in the presence of distinct oceanographic features in the foraging area and their exploration by king penguins, local bathymetry and its impact on ACC circulation patterns may lead to differences in local oceanography at both study locations. Local habitat has been shown to account for significant differences in foraging profitability among colonies (Karnovsky et al. 2011; Sharples et al. 2012), as it defines the oceanographic structure and therewith prey distribution patterns of the animals' foraging area. Myctophids, king penguins main prey, are known to be highly sensitive to thermal conditions in their environment (Hulley 1981; Pusch et al. 2003; Collins et al. 2008; Collins et al. 2012; Fielding et al. 2012). Myctophid distribution and behavioural patterns of animals exploring such prey resources are therefore strongly determined by the local oceanographic habitat, and are likely to vary between different breeding locations even though larger-scale similarities in oceanographic and behavioural patterns may exist.

At both our study locations, bathymetry plays an important role in the steering of ACC flows as well as the occurrence of mesoscale oceanographic features (Moore et al. 1997;

Moore et al. 1999b; Trathan et al. 1997; Trathan et al. 2000; Park et al. 2008b). However, while the large spatial extension of the Kerguelen Plateau to shallow depths is directly impacting horizontal and vertical circulation processes throughout the entire water column (Park et al. 1998; Park et al. 2008b; van Wijk et al. 2010), the area to the north of South Georgia is of a more pelagic nature characterized by greater depths. In these conditions, bathymetry may impact the upper water column mostly through horizontal steering defining ACC flows and mesoscale features, and only to a lesser extent through vertical processes such as upwellings reaching the ocean surface as occur in proximity to the Kerguelen Plateau. The differences in the oceanographic structure of the foraging habitat in both breeding locations, and the driving forces defining such differences are likely to be reflected in prey distribution patterns, and in the foraging behaviour of marine predators exploring such prey resources.

Role of vertical processes: differences between South Georgia and Kerguelen

Vertical processes such as bathymetry-related upwellings into the upper water column associated with low geostrophic velocities appeared to constitute a major foraging feature for king penguins breeding at Kerguelen, whereas king penguins at South Georgia explored more oceanic structures characterized by strong horizontal dynamics and increased geostrophic velocities such as frontal flows and eddies (see Fig. 7.4a; see also Trathan et al. 2008; Scheffer et al. 2010). Both these processes, vertical dynamics at upwellings as well as horizontal dynamics at fronts and eddies, are known to be associated with elevated biological productivity (Franks et al. 1992; Lima et al. 2002), and are thought to represent profitable foraging areas for marine predators (Rodhouse et al. 1996; Yen et al. 2006; Cotte et al. 2007; Baylis et al. 2008; Bost et al. 2009; Bailleul et al. 2010). Diving behaviour further suggests the exploration of less profitable prey resources at Kerguelen (see Fig. 7.4b), with longer bottom periods at all dive depths indicating less

accessible prey requiring more time investment for foraging (Charrassin et al. 2002, see Fig. 7.5) throughout the water column.

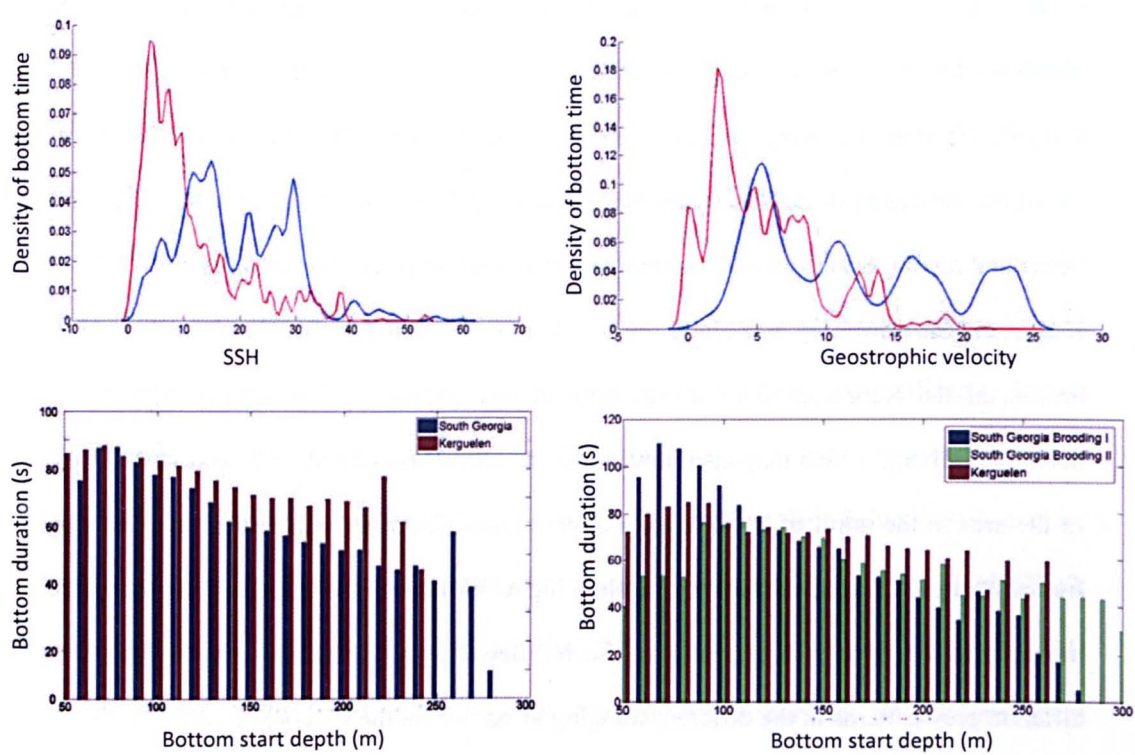


Figure 7.4: a - Bottom periods of foraging king penguins at South Georgia (blue line) and Kerguelen (red line) spent in different geostrophic velocities. b – Bottom duration in relation to bottom start depth of king penguins at South Georgia (blue & green bars) and Kerguelen (red bars).

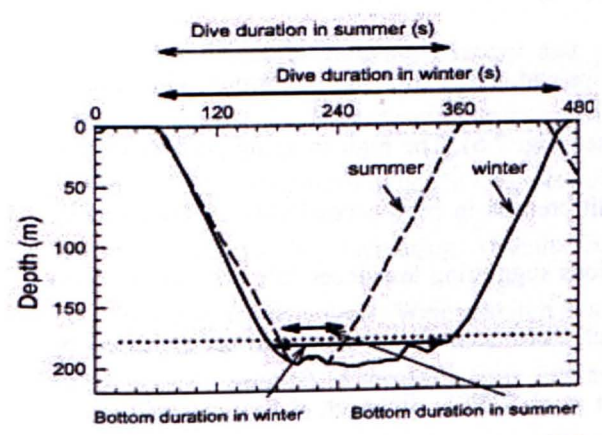


Figure 7.5: Relation of time spent in the bottom phase and seasonal changes in prey availability, assuming variable prey availability in terms of density and/or energetic value at a given depth. Low prey availability during winter leads to longer bottom times. Figure from Charrassin et al. 2002.

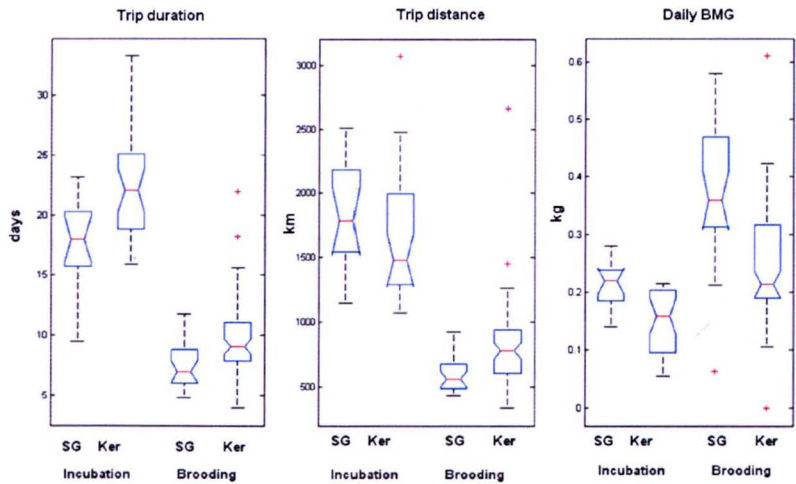
The area along the south-eastern Kerguelen Plateau shelf break may provide for profitable prey resources associated with the upwelling of southern waters to shallow depths, which is known to be explored by a range of marine predators breeding on the Kerguelen Plateau (Hindell et al. 2011). However, our study suggests that these resources may be less profitable for foraging king penguins than those encountered at South Georgia in terms of foraging trip time necessary for exploitation as well as in terms of daily BMG. Maximum biological productivity has been reported to occur at locations of combined vertical and horizontal mixing through upwelling and horizontal flow dynamics (Martin et al. 2002). At Kerguelen, the upwelling area along the south-eastern Kerguelen shelf break is situated in the lee of the Kerguelen Plateau, resulting in low geostrophic velocities and reduced horizontal mixing, which may also impact prey resources associated with such upwellings. In the area to the north of South Georgia, the strong horizontal and vertical dynamics of frontal juxtaposition and eddies may result in higher biological productivity and potentially more profitable myctophid aggregations. Such differences in profitability may be related to different prey patterns in the different foraging areas, where the PF core or eddies at South Georgia may provide for prey resources of high densities (Kozlov et al. 1991; Rodhouse et al. 1996). Alternatively, it may be related to prey of different energy content, which may result from different prey sizes or different maturity stages or different species exploited. However, this hypothesis remains speculative due to insufficient data on myctophid distribution and their consumption by king penguins.

Brooding birds showed shorter foraging trips and higher foraging performance in terms of daily body mass gain at South Georgia (see Fig. 7.6). The high foraging performance of South Georgia birds may be related to differences in prey accessibility as indicated by diving behaviour, with longer bottom periods suggesting less accessible prey from depths >150 m at Kerguelen (see Fig. 7.5b), but more accessible than at Crozet indicated by deeper dives during brooding (Charrassin et al. 1999). However, the strong habitat and

behavioural segregation during brooding may also improve adaptation of foraging strategy to prey distribution and breeding constraints, which may allow better prey exploration and ultimately lead to overall improved foraging performances. Different environments characterized by the presence of different oceanographic features have been suggested to play important roles in prey accessibility and therefore foraging behaviour and profitability of marine predators (Muelbert et al. 2012). Specifically the distance to profitable feeding grounds from the breeding location (Sharples et al. 2012) and the profitability of prey resources associated with oceanographic features accessible from the colony (Karnovsky et al. 2011) have been found to play important roles in foraging strategy and behaviour as well as for the profitability of foraging trips. Bathymetry is known to significantly impact oceanography and prey patterns in a given area, and has been found to be a major driving force for the foraging strategy of marine predators adjusting their behaviour to explore prey resources associated with bathymetry-related features (Campagna et al. 2000; Campagna et al. 2007; Chapman et al. 2004; Baylis et al. 2008; Wingfield et al. 2011; Muelbert et al. 2012). At the Kerguelen Plateau, the importance of the prominent bathymetry on foraging behaviour has been suggested for king penguins (Bost et al. 2011) and other marine predators (Lea et al. 2008; Hindell et al. 2011). Our study confirms bathymetry to be a major factor driving foraging behaviour of king penguins breeding at Kerguelen. It furthermore suggests that the foraging habitat differences between our breeding locations, which appear to be at least partly determined by local bathymetry, may lead to differences in foraging strategy and profitability, confirming studies on other marine predators. However, despite the inter-colony differences in foraging behaviour and performance, the long-term trends in king penguin numbers in both breeding colonies have been reported to be increasing (South Georgia: Woehler & J.P.Croxall 1997; Kerguelen/Ratmanoff colony: Weimerskirch et al. 1989; Chamaillé-James et al. 2000; Bost et al. 2012) in relation to recovery from human disturbances and major unsteadiness in

trophic webs, see Bost et al. 2012. This implies that current oceanographic conditions and associated prey resources are particularly adequate for the successful raising of chicks in both locations. The observed behavioural differences and the apparent sufficient foraging performance in both locations may reflect strong behavioural flexibility of king penguins in order to adapt foraging to local habitat conditions in order to maximize foraging performance.

Figure 7.6: Foraging trip characteristics (trip duration and length) and daily body mass gain (BMG) for incubating and brooding king penguins at South Georgia (SG) and Kerguelen (Ker).



7.3 Adaptive capacities and susceptibility of king penguins towards environmental variability and climate change

King penguins showed high inter-and intracolony behavioural flexibility, adjusting foraging behaviour to different environments and changing breeding constraints. The selective exploration of distinct oceanographic features in the foraging habitat depending on local oceanography and breeding constraints may indicate high adaptive capacities of king penguins towards variability in environmental conditions in the foraging area. However, while seabirds are known to be able to buffer variability in environmental conditions and prey availability through flexibility in foraging behaviour (Peron et al. 2012), thresholds may exist whereby such foraging flexibility can no longer buffer

reproductive success against low food availability (Dall & Boyd 2002; Ronconi & Burger 2008). The breeding season 2009/10 at Kerguelen indicated such limits in the buffering of environmental variability through behavioural flexibility for king penguins, showing the possible drastic effects of surpassing the animals' adaptive capacities on reproductive success. The identification of critical environmental conditions triggering such threshold responses is important for understanding limiting factors in marine ecosystems and the potential impact of future environmental changes on these systems, which has important implications for conservation and ecosystem management. The investigation of king penguins behaviour in two breeding locations under different environmental conditions and constraints over several years allowed us to identify oceanographic features of key importance for foraging king penguins, the Polar Front and cold-water influx of southern origin (the SACCF at South Georgia, and the Fawn Trough Current subsurface current at Kerguelen) at large scales, and eddies and bathymetry-related upwellings at mesoscales. Such identification of key features explored during foraging may help to better understand critical environmental factors impacting such key features and associated prey resources when triggering threshold responses. Such results may be of particular importance when taking into account information from the observed threshold response situation during the catastrophic breeding season 2009/10 at Kerguelen, which has helped in identifying key features of successful foraging, and qualify and quantify environmental conditions leading to such threshold responses in king penguins.

Changes in oceanographic features related to climate change have been suggested to significantly impact king penguins foraging behaviour and at-sea distribution, with the foraging behaviour of king penguins breeding at Crozet directly reflecting latitudinal southward shifts in the PF position (Peron et al. 2012). Our study confirms the importance of the PF for foraging king penguins at South Georgia and Kerguelen as suggested by earlier studies (Bost et al. 1997; Guinet et al. 1997; Trathan et al. 2008; Bost et al. 2009;

Scheffer et al. 2010; Peron et al. 2012). Particularly the interannual changes in foraging behaviour in relation to the PF position at Kerguelen may indicate the importance of the PF variability for foraging king penguins, with southward shifts negatively impacting foraging performances in terms of trip characteristics, diving behaviour and body mass gain (see Chapter 6). However, in addition to the PF, our study also points out the importance of oceanographic features independent of the PF for foraging penguins. For breeding colonies located to the south of the PF such as South Georgia and Kerguelen, the cold-water features of southern origin in proximity of the islands appear to represent such additional key features. King penguins may therefore not only be affected by variability of the PF, but also by changes in such other key oceanographic features in their foraging area, which may in turn be impacted by the variability of the adjacent PF. Prey resources associated with these cold-water features and their interaction with the PF may even be of higher importance than the PF itself, as indicated by the breeding season 2009/10 at Kerguelen. The shift of the cold-water influx from the FTC to the south of the foraging area of king penguins resulted in drastically reduced foraging performances, where extended foraging trips following the PF path may indicate that the PF in proximity of the colony may not have provided for sufficiently profitable prey resources to sustain efficient foraging. However, this may also have been related to changes in prey resources at the PF due to the warm-water intrusions in the upper ocean during the breeding season 2009/10 at Kerguelen (see Chapter 5).

Despite their behavioural flexibility, king penguins appear to have limits of behavioural adaptation to changes in environmental conditions and prey resources. While our inter-colony comparison indicates high behavioural flexibility in adapting to different environmental conditions, the breeding season 2009/10 clearly showed the limits of such adaptive capacities to maintain successful foraging and chick raising. Current climate change projections predict a general warming of the oceans (Solomon et al. 2007), which is

thought to be particularly pronounced in the Southern Ocean. Changes in the distribution of environmental parameters such as the mean and variance lead to non-linear changes in the frequency and amplitude of extreme events due to shifts in the distribution tails (Meehl et al. 2000; Jentsch et al. 2007, see Fig. 7.7). Facing ongoing climate change and future warming of the oceans (Gille 2002; Solomon et al. 2009), extreme events are predicted to

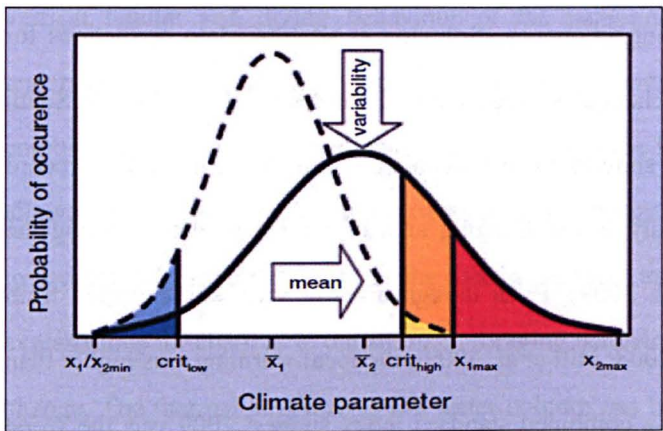


Figure 3. Expected changes in the probability of occurrence of extreme weather events under climate change for any given climate parameter (eg precipitation, temperature). From scenario A (dotted line; eg today) to scenario B (solid line; eg year 2050), mean value (\bar{x}_1 to \bar{x}_2) and overall variability (standard deviation or width of the curve) increase. The probability of situations exceeding critical thresholds (crit_{low} and $\text{crit}_{\text{high}}$) changes dramatically; for example, $\text{crit}_{\text{high}}$ shifts from including only the yellow area to including the whole orange and red area. Unprecedented extremes occur (red area) as novel maxima are reached ($x_{1\text{max}}$ to $x_{2\text{max}}$). On the other hand, current minima become less probable (light blue to dark blue). All alterations stress the increasing significance of extreme events with gradual shifts of climatic parameters. Note that the overall pattern will prevail, even if other probability distributions are appropriate. Adapted from Meehl et al. (2000).

Figure 7.7: Expected changes in the probability of occurrence of extreme weather events under climate change for any given climate parameter such as for example temperature. Figure from Jentsch et al. (2007).

become more likely (Alley et al. 2003; Jentsch et al. 2007; Solomon et al. 2007; Jentsch & Beierkuhnlein 2008). Intensification of weather extremes is currently emerging an important aspect of climate change, and research on extreme events (event-focused in contrast to

trend-focused) has increased in recent years (Jentsch et al. 2007).

Investigating ecosystem or species reactions towards extreme events and evaluating critical environmental conditions where systems or components can not adjust anymore, and the underlying causes for these critical points is an important issue. The 2010 event allows insights into key elements of successful foraging of king penguins breeding at Kerguelen, and into possible reactions towards pronounced changes in their foraging habitat.

Extreme weather events have been shown to negatively affect marine predators such as the survival of fur seal pups (Forcada et al. 2005; Lea et al. 2009) and seabirds (Frederiksen et

al. 2008). In threatened seabirds, extreme events are thought to lead to a higher probability of extinction through increasing process variance in survival (Frederiksen et al. 2008). Our study confirms the negative impact of extreme environmental events on king penguins breeding at Kerguelen in terms of foraging and reproductive success, which is ultimately impacting survival. It therefore underlines the importance of including the impact of extreme events and their increasing frequency (Solomon et al. 2007) into predictions for the ecological effects of climate change as suggested by Frederiksen et al. 2008. At South Georgia, penguins and fur seals showed lowest weaning and fledging masses on record during a local warm SST anomaly in the foraging area of marine predators during the breeding season 2009 (Hill et al. 2009). Even though a warm year was expected from remote impacts (Meredith et al. 2008; Hill et al. 2009), the local warming was higher than expected, and predator data and a combined standard index suggest 2009 was the worst year on record with only 1994 being comparable (Croxall et al 1999; Hill et al. 2009). It has been suggested that the warm SST anomaly may have been caused by intense in situ heating of the mixed layer as a consequence of local atmospheric effects (Hill et al. 2009). Such patterns of local upper-ocean warming and extreme effects on marine predators, potentially also through alterations in prey distribution, may be similar to the situation and mechanisms at Kerguelen during February 2010.

Our study shows the impact of environmental variability, particularly in the PF and FTC position, on king penguins breeding at Kerguelen in terms of surface and diving behaviour. King penguins breeding at Crozet have already been reported to be impacted by changes in the PF position (Peron et al. 2012) and sea ice retreat (Le Bohec et al. 2008). Our study confirms this hypothesis for king penguins breeding at Kerguelen. However, bathymetry-oceanography interactions at Kerguelen appear to induce non-linear responses of key oceanographic features and associated prey resources to PF southward movements, potentially leading to drastic changes in king penguins foraging behaviour from critical PF

southward positions in the area to the SE of Kerguelen. Studies of the impact of climate change on king penguins breeding at Crozet were based on survival rates (Le Bohec et al. 2008), but in future analyses it may be necessary to take into account other important factors affecting king penguins' population growth (Barbraud et al. 2008). Studies based on surface behaviour only (Peron et al. 2012) do not take into account changes in the vertical habitat and diving behaviour of the penguins, which play crucial roles for understanding animals' behaviour towards environmental variability. In this study, the combination of behaviour and habitat descriptors in the horizontal and vertical dimension allowed us to gain more detailed insights into king penguins foraging behaviour in relation to oceanographic conditions at the ocean surface and at depth, and find possible explanations for changes in the animals' foraging behaviour associated with environmental change. The thermal structure of the water column has been shown to play a key role for diving predators (Brill et al. 1993; Brill & Lutcavage 2001; Cartamil & Lowe 2004; Scott & Chivers 2009) and king penguins in particular (Charrassin & Bost 2002; Scheffer et al. 2012). Significant changes in diving behaviour and vertical foraging habitat use by king penguins breeding at Kerguelen associated with environmental variability underlines the importance of oceanographic conditions at depth for the birds. Taking into account the variability in the vertical foraging habitat and behavioural adaptations of the animals should therefore lead to a more comprehensive understanding of the reactions of diving predators towards environmental change.

King penguin populations have increased since the 1960's (Woehler et al. 2001; Delord et al. 2004) despite warming of the Southern Ocean (Solomon et al. 2007). Our study shows that king penguins are adjusting their behaviour to the environmental conditions encountered, presumably enabling them to buffer reproductive success and population survival towards environmental variability. However, it appears that such adaptive capacities can buffer changes in environmental conditions only to a certain extent and that

threshold conditions may exist, limiting the animals' capacities to buffer reductions in prey availability by adaptations in foraging behaviour (Harding et al. 2007). Marine predators have been reported to exhibit non-linear threshold-type responses to changes in prey availability (Cairns 1987), where small changes in prey trigger rapid changes in adult survival, reproductive performance and/or foraging behaviour (Harding et al. 2007; Piatt & Sydeman 2007). Even small changes in oceanographic features and prey distribution associated with climate change may therefore lead to significant changes in foraging behaviour of king penguins, which may ultimately be reflected in the reproductive success of the animals. This effect may be enhanced by non-linear responses in oceanographic conditions and prey availability to changes in environmental conditions, as it appears to be the case in the area to the south-east of Kerguelen.

7.4 Conclusion and future research perspectives

This work has improved our knowledge about the foraging behaviour of a top marine predator of the Southern Ocean, the king penguin, in relation to its environment. Through the study of the species in two distinct locations it allowed me to generate important new insights into the detailed behaviour of king penguins in relation to their oceanographic environment, and further enabled me to identify potential key oceanographic features for profitable foraging, and finally how the species may respond to changes in these features in the future.

The most important results of this thesis are as follows:

- The Polar Front (PF) and cold-water features of southern origin (the southern ACC Front, SACCF at South Georgia, and the Fawn Trough Current, FTC at Kerguelen) were key large-scale features used during foraging at both study locations.
- Eddies and bathymetry-related upwellings were important mesoscale features explored during foraging.
- The main features at depth explored during foraging phases were the thermocline and Winter Water (WW). However, king penguins at both breeding locations also foraged in Circumpolar Deep Water (CDW), which appears to become more important when birds are under increased constraints.
- Variability in the PF and in the cold-water features in the foraging area significantly affected king penguins foraging behaviour. Southward shifts in the PF and the FTC in the foraging area of king penguins breeding at Kerguelen resulted in altered foraging behaviour and low reproductive success during one breeding season.

One important challenge for ecologists in the 21st century is to understand and predict the potential effects of environmental change on biological communities. In this context, understanding the foraging behaviour and the identification of potential key features for successful foraging by king penguins is indispensable. Understanding and predicting how marine predator populations will respond to habitat change will be essential for developing conservation management strategies. Responses of animals to variability in their habitat as well as to previous and current environmental change may give important information for the development of predictive models. Such models may be developed taking into account horizontal habitat descriptors such as SST, SSH and/or bathymetry, but they will also need to take into account the vertical structure of the ocean. The results of this thesis provide detailed information on how king penguins explore their habitat in both horizontal and vertical dimensions, and highlights key structures at the ocean surface and at depth. Future studies building on this work may therefore include predictive habitat modelling in the horizontal and vertical dimension, building on results from my thesis work.

Due to time constraints and the magnitude of the task for the complete analysis of the tracking data from Kerguelen (with different temporal and spatial data resolution recorded by different devices used over the course of the long-term king penguin monitoring programme resulting from different types of ARGOS devices, GPS devices, and TDR devices), as well as the large datasets of behavioural and oceanographic data in 3 dimensions, I was not able to analyze the entire Kerguelen tracking dataset. Analysis of the remaining years will undoubtedly add information to the results of this work, underlining patterns that have emerged from my study.

The study of potential responses of king penguins breeding at South Georgia to interannual changes in their environment was restricted by the limited number of study years. Additional fieldwork on king penguins breeding at South Georgia would allow valuable

insights into the potential impact of such interannual variability in oceanographic conditions on the animals breeding there, which may add important information to my results and hypotheses concerning the foraging behaviour of king penguins resulting from my study.

Advances in biologging technology will also result in more complete and continuous datasets, and improve the spatial and temporal resolution of tracking data. In this context the future use of GPS loggers may be of particular importance, as the resulting datasets will allow for more detailed study of surface behaviour with considerably reduced uncertainties due to data gaps. This may allow the use of more sophisticated modelling methods such as state-space modelling, where behavioural modes of the animals can be inferred from changes in surface behaviour. In my study, the use of such methods was restricted by the low spatial resolution of tracking data obtained by ARGOS devices. Future work on high-resolution GPS datasets would facilitate this approach, which may be further improved by incorporating environmental covariates into the models. Such modelling may be carried out in the horizontal dimension as used for a number of study species (Jonsen et al. 2003; Jonsen et al. 2005; Breed et al. 2009), but may also include most recent developments of state-space modelling based on behaviour and environmental covariates for the vertical dimension (Bestley et al. 2012). In both instances, results from this study will provide important information about key oceanographic structures and environmental variables for foraging king penguins, which may facilitate the development of such models including the horizontal and vertical dimension of the animals' environment.



To be continued...

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Annexes: related published research articles

Article 1: Scheffer A, Trathan PN, Collins M (2010) Foraging behaviour of King Penguins (*Aptenodytes patagonicus*) in relation to predictable mesoscale oceanographic features in the Polar Front Zone to the north of South Georgia. *Progress In Oceanography* 86:232-245. (Article submitted during my MSc project work, but revised based on results from the PhD work.)

Article 2: Scheffer A, Bost CA, Trathan PN (2012) Frontal zones, temperature gradient and depth characterize the foraging habitat of king penguins at South Georgia. *Marine Ecology Progress Series* 465:281-297.

Article 3: Bost CA, Goarant A, Scheffer A, Koubbi P, Duhamel G, Charrassin JB (2011) Foraging habitat and performances of King penguins *Aptenodytes patagonicus* Miller, 1778 at Kerguelen islands in relation to climatic variability. In: Duhamel G, Welsford D (eds) *The Kerguelen Plateau: marine ecosystem and fisheries, Proceedings of the 1st international Science Symposium on the Kerguelen Plateau* Société Française d'Ichtyologie, Paris, p 199-202.

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Foraging behaviour of King Penguins (*Aptenodytes patagonicus*) in relation to predictable mesoscale oceanographic features in the Polar Front Zone to the north of South Georgia

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ARTICLE INFO

Article history:
Received 13 March 2008
Received in revised form 1 December 2009
Accepted 10 April 2010
Available online 8 May 2010

ABSTRACT

Marine predators are thought to utilise oceanic features adjusting their foraging strategy in a scale-dependent manner. Thus, they are thought to dynamically alter their foraging behaviour in response to environmental conditions encountered. In this study, we examined the foraging behaviour of King Penguins (*Aptenodytes patagonicus*) breeding at South Georgia in relation to predictable and stable oceanographic features. We studied penguins during their long post-laying foraging trips during December 2005 and January 2006. For this investigation, we undertook a simultaneous analysis of ARGOS satellite-tracking data and Mk 7 Wildlife Computers Time Depth Recorder (TDR) dive data. To investigate correlations between foraging behaviour and oceanographic conditions, we used SST data from January 2006 from MODIS satellite AQUA. To determine changes in search effort, first passage time (FPT) was calculated; for analysis of dive behaviour, we used several dive parameters that are thought to be reliable indicators of changes in foraging behaviour. King Penguins appeared to target predictable mesoscale features in the Polar Front Zone (PFZ), either a warm-core eddy in the PFZ or regions of strong temperature gradients at oceanic fronts. Two different trip types could be distinguished: direct trips with a straight path to one foraging area at the edge of an eddy or at a thermal front, and circular trips where birds foraged along strong thermal gradients at the northern limit of the PFZ. It is likely that both trip types were a direct consequence of prey encounter rates and distributions, both of which are likely to be associated with these oceanographic features. Circular trips often included passages across the centre of an eddy where birds made deep foraging dives, but remained only a short time in the eddy, possibly because prey were too deep. All birds showed Area Restricted Search (ARS) at scales of <10 km. The two trip types had different ARS patterns, with clear ARS hotspots for direct trips and several ARS hotspots over the whole duration of the trip for circular trips. Dive behaviour had clear relationships with the changing water temperature and the time of day, presumably in response to different prey distribution. Especially for direct trips, dive behaviour showed significant differences within and outside of ARS hotspots. Thus, King Penguins appear to target predictable mesoscale features in the PFZ. They use ARS in different patterns to exploit the environment and adjust their foraging strategy and diving behaviour depending upon conditions they encountered. Diving behaviour showed correlations to ARS patterns, especially for direct trips, which may represent a favourable foraging strategy. The presence of predictable oceanic features allows King Penguins to focus their foraging effort, presumably allowing them to increase their foraging success and decrease their diving effort.

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1. Introduction

The survival and breeding success of seabirds and other marine predators critically depends upon the spatial and temporal distribution of their prey; indeed, their foraging behaviour is strongly related to the abundance, distribution and predictability of these resources (Rodhouse et al., 1996; Hull et al., 1997; Weimerskirch et al., 1997; Fauchald et al., 2000; Weimerskirch, 2007).

Physical and biological processes in the ocean control the distribution and abundance of plankton and nekton, which affects the distribution of higher trophic levels such as seabirds and marine mammals (Pakhomov and McQuaid, 1996). Heterogeneity in the marine environment results in patchiness and aggregated distributions of marine resources over several different scales (Croxall et al., 1984; Fauchald, 1999). Foragers in patchy systems are known to adjust their search pattern in order to assess the system at different scales (Fauchald, 1999). Marine predators feeding on such prey patches should concentrate their foraging efforts in areas where resources are most predictable and therefore adjust their

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foraging behaviour at different scales depending on the conditions encountered (Weimerskirch et al., 1997; Fauchald et al., 2000; Pinaud and Weimerskirch, 2005; Weimerskirch, 2007). Polar and temperate waters can be highly productive and contain predictable oceanographic structures and prey resources (Weimerskirch, 2007). Therefore, marine predators in the Southern Ocean can rely on these predictable oceanographic features and the associated prey resources.

With the development of satellite tracking and other bio-logging techniques it is now possible to obtain detailed insights into predator–prey dynamics and predator foraging strategies including the diving behaviour of marine predators. Such methods have so far mainly concentrated on flying seabirds (Weimerskirch et al., 1997; Nel et al., 2001; Pinaud and Weimerskirch, 2005; Weimerskirch, 2007) and other marine predators (Block et al., 1997; Campagna et al., 1998; Bailleul et al., 2007; McMahon et al., 2007; Teo et al., 2007) and less is known about the fine-scale foraging behaviour and spatial patterns of diving seabirds such as penguins. King Penguins (*Aptenodytes patagonicus*) constitute an important component of the Southern Ocean marine food web (Woehler, 1993). They breed on many of the sub-Antarctic islands (Williams, 1995) in the proximity of the Polar Frontal Zone (PFZ). There are important aggregations breeding at Marion, Prince Edward, Crozet, Kerguelen, Heard, Macquarie, South Georgia and the Falkland Islands. Estimates of the world population (Woehler, 1993) are updated by current estimates that suggest 2000,000 breeding pairs (Available at: <http://www.penguins.cl/king-penguins.htm>) however population numbers have changed rapidly over recent years and the actual world population size is unknown. For example, the colony at St. Andrews Bay, South Georgia comprised only 700 pairs in 1928 (Kohl-Larsen, 2002); today the same colony is sufficiently large that it may comprise upwards of 150,000 pairs (Trathan et al., 2007).

Together with Emperor Penguins (*Aptenodytes forsteri*), King Penguins are known to be the most pelagic of all penguins (Kooyman and Kooyman, 1995) and are able to spend several weeks at sea during their extended foraging trips (Kooyman et al., 1992;

Wilson, 1995; Pütz et al., 1998). This makes them highly dependent on oceanographic mesoscale features of the open ocean, which in turn are often determined by rugged topography and bathymetric features. Flying seabirds are able to cross extended areas of the ocean (Weimerskirch et al., 1997; Pinaud and Weimerskirch, 2005) and can therefore search for prey at large scales. In contrast, diving seabirds such as penguins generally travel more slowly and with higher energy costs per unit travel-swimming is more energetically costly than flying or gliding (Maina, 2000; Lovvorn and Liggins, 2002). Diving seabirds also have a much lower radius of prey detection due to reduced visibility underwater. Therefore, penguins need to rely on predictable prey resources that may be associated with detectable oceanographic features.

The island of South Georgia is situated to the north of the Scotia Sea south of the Polar Frontal Zone (PFZ; Fig. 1). The PFZ is a complex, circumpolar transition region between the Antarctic and Antarctic surface waters. It is generally highly dynamic and is characterised by the presence of numerous eddies and meanders (Gordon et al., 1977; Glorioso et al., 2005). Production within frontal zones is often elevated compared to that in surrounding oceanographic areas (Thomas and Emery, 1988). Such production can be spatially extensive and temporarily stable over several weeks with a certain scale-dependent predictability (Weimerskirch, 2007).

King Penguins are known to forage preferentially along large-scale physical features such as oceanographic fronts (Bost et al., 1997) and to use hydrographic features in the vertical dimension to exploit the water mass in three dimensions (Charrassin and Bost, 2001). In the South Indian Ocean, they are also able to adjust their foraging activity and utilise specific oceanographic areas for non-random foraging (Charrassin and Bost, 2001; Cotté et al., 2007).

King Penguins are highly specialised diving birds (Kooyman and Ponganis, 1990); they spend nearly 50% of their time at sea underwater (Charrassin et al., 1998). It is assumed that they are visual feeders and need a certain ambient light level to detect their prey underwater (Pütz et al., 1998; Bost et al., 2002). King Penguins depend upon the distribution of myctophid fish that constitute their main prey (Cherel and Ridoux, 1992; Olsson and North, 1997;

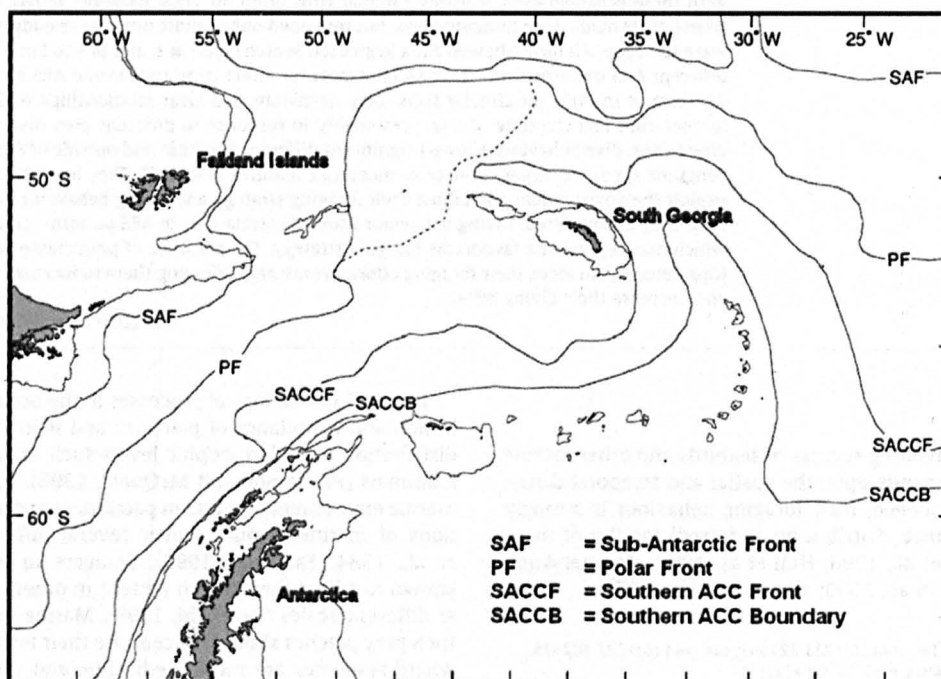


Fig. 1. Location of the island of South Georgia in the Southern Ocean, with the main fronts of the Antarctic Circumpolar Current (after Orsi et al. (1995) and Trathan et al. (1997, 2000)).

Cherel et al., 2002; Bost et al., 2002) and which undertake diurnal vertical migrations (Zasel'slii et al., 1985; Bost et al., 2002). Previous studies have suggested the existence of close relationships between penguins' foraging activity and time of day, with deep dives during daylight and shallower dives during night-time (Wilson, 1995; Kooyman et al., 1992; Pütz et al., 1998; Bost et al., 2002). Indeed, penguin foraging behaviour can be identified by a number of dive parameters (Kooyman et al., 1992; Pütz et al., 1998, 2006; Pütz and Cherel, 2005; Bost et al., 2007) calculated from satellite and time–depth–temperature recorder (TDTR) data.

This study investigates the foraging strategy of King Penguins breeding at South Georgia in relation to both the time of day and variation in sea surface temperature (SST). We also explored how penguins encounter predictable oceanographic mesoscale features in the PZF to the north of South Georgia, and how they adjust their dive behaviour and foraging activity as a consequence. We undertook a simultaneous analysis of ARGOS satellite-tracking data and TDR dive data allowing insights into trip orientation, bird movement in relation to oceanographic mesoscale features as well as detailed analysis of several dive parameters that are thought to be reliable indicators of changes in diving behaviour.

2. Materials and methods

2.1. Device deployments

Between December 2005 and January 2006, 11 female King Penguins breeding at the Hound Bay colony in the north-east of South Georgia (54°23'S, 36°15'W) were tracked during their long, post-laying foraging trips. The birds were equipped with ARGOS satellite transmitters (SPOT 4 Platform Transmitter Terminals, Wildlife Computers, Redmond, USA) as well as with Mk 7 (Wildlife Computers) time–depth recorders. Devices were attached following methods modified from Wilson et al. (1997); briefly, devices were attached using waterproof Tesa® tape and quick-drying two-part glue. To aid in the recovery of devices, all birds were marked on their front with permanent black hair dye and all devices were painted yellow. All devices were recovered after a single foraging trip. Attached devices may have negative impacts on the hydrodynamics of swimming (Wilson et al., 2004) but in our study, there was no significant difference in trip duration between instrumented and control birds (see Trathan et al., 2008).

2.2. Sea surface temperature data

Sea surface temperature data for the study area (between 48°S and 30°W) were obtained from MODIS AQUA satellite (NOAA, Available at: <http://modis.gsfc.nasa.gov/>) for the month of January 2006. A composite map for the period was created with a spatial resolution of 0.04167° latitude and longitude. The foraging tracks of all birds were plotted on the SST map of the region to visualize potential correlations with oceanographic features at different scales.

2.3. Satellite tracking

The horizontal movements of penguins at sea were tracked by ARGOS satellite telemetry. The devices were set to transmit continuously when dry, with a repetition rate of 45 s. Three classes of accuracy were obtained with the ARGOS system: class 3 with accuracy 150 m; class 2 with accuracy 350 m and class 1 with accuracy 1 km (http://www.argos-system.org/html/system/faq_en.html#LOCATION%20ACCURACY). Locations with accuracy A, B or Z were not used in this study (1.15% of positions); these positions can have

variable accuracy and were not required with respect to the scale needed to analyse the general form of the tracks.

Trips were classified into two types according to the differences in trip course identified from satellite data: direct trips which targeted one limited area, and circular trips where birds moved along strong temperature gradients and targeted multiple areas. For each bird, we calculated trip duration, distance covered, mean and maximum distance to the colony. Surface speed between two ARGOS locations was calculated by assuming travel in a straight line with constant surface speed (Weavers, 1992). Since the maximum travel speed of a King Penguin is 14 km/h (Kooyman and Davis, 1987), speeds higher than 14 km/h were rejected.

To determine changes in search effort of the tracked birds, first passage time (FPT) was calculated following Fauchald and Tveraa (2003) at different spatial scales of radius 1–128 km. To calculate FPT, track positions were interpolated at temporal resolution of 5 min; locations where the radius at a given spatial scale overlapped with either the start or the end of the track were removed. Variance maxima of FPT $S(r) = \text{Var}(\log(t(r)))$ indicated the spatial scale of slowest passage time and of highest search effort, where r is the radius of the circle and $t(r)$ the time lag between the first passage time of the circle backward and forward along the path. To locate areas with the highest search effort in each trip, FPT was plotted as a function of time since departure from colony (Fauchald and Tveraa, 2003). Areas of the upper quartile values of FPT represent the areas with the slowest passage time and the most intense search effort and were designated as 'ARS hotspots'.

2.4. Time–depth recorders: analysis of diving behaviour

Time and depth data were recorded at 1 Hz and stored in a 2 Mb Flash EPROM chip. During long surface intervals, recording was halted by a saltwater switch and resumed when the bird restarted diving activity. The resolution of dive data recording was 0.5 m. To avoid the analytical complications associated with surface wave clutter, dives less than 3 m were removed from the analysis. Dives were classified as either foraging (>20 m depth; Pütz and Cherel, 2005) or travel dives. With a combination of the dive profiles from TDR data and the PTT tracks overlaid on the SST map, correlations relating to trip type, diving behaviour and oceanographic conditions could be determined.

Dive analyses were carried out on 1400 randomly selected dives per bird using Matlab software (The MathWorks, Inc., Natick, MA, USA). For each dive we determined maximum dive depth, dive duration, duration of the prior surface interval and post-dive interval, number of reversals (i.e. number of changes in depth direction during the dive, either increasing or decreasing), bottom duration (i.e. time spent at 75% of the dive depth) and bottom activity (i.e. vertical distance travelled during bottom period). We assessed changes in dive frequencies and the above dive parameters in relation to the time of day and SST during the trip to determine whether there were major differences between the trip types in several dive parameters and to determine the conditions under which the different trip types were carried out. Geographical coordinates for each dive start were interpolated from satellite-tracking data, assuming straight-line travel and constant speed between two location points (Weavers, 1992). The sea surface temperature values at each dive location were estimated by searching for the geographically nearest value within the SST satellite dataset; this allowed us to determine changes in diving behaviour associated with changes in SST and oceanographic features encountered during the trips.

To evaluate changes in diving behaviour with the time of day and changing SST, dive activity (dives/h) during different daytime periods (daytime, twilight and night-time) was calculated for the different SST values. For each dive, we assigned one of the daytime periods. Exact times for sunrise and sunset were calculated for

each dive location based on the interpolated geographical coordinates (Sea_Air Matlab Code, Woods Hole Oceanographic Institution, Woods Hole, MA, USA). For twilight hours, we used the nautical twilight definition (US Naval Observatory Astronomical Applications Department), with dawn and dusk defined as the centre of the sun being geometrically 12° below the horizon. Because of light absorption in water, underwater twilight hours were defined as the nautical twilight hours but with a 90 min shift towards daylight. Midday was defined as the period between 11:00 and 13:00 in order to test specific characteristics and changes in diving behaviour around midday.

To identify correlations in diving behaviour with surface tracks and search behaviour, several dive parameters were compared within the ARS hotspots (dives within the upper 25% of FPT) and outside the ARS hotspots. In order to determine differences between the different trip types, these comparisons were carried out separately on the dives for direct trips and the dives for circular trips. To evaluate the influence of latitude (and changing SST) on foraging behaviour, the number of foraging dives within and outside of the ARS hotspots was calculated in relation to latitude.

2.5. Statistical analysis

To compare diving behaviour between the two trip types, between ARS hotspots and other areas, as well as the throughout the day, we used Kruskal–Wallis tests. We chose a nonparametrical test to cope with possible autocorrelation in the data. To test differences in parameters calculated from satellite data (trip duration, distance travelled, distance from colony) we used two-sample *t*-tests.

3. Results

3.1. Trip orientation in relation to SST and mesoscale oceanographic features

All trips were oriented to the north towards the PFZ waters or regions on its northern limit. Many trips appeared to target mesoscale oceanographic features in these areas. Travel at the start and end of each trip was across waters of 2–4 °C; those periods were characterised by straight headings for all birds and elevated travel speed with short surface intervals (Table 1). When birds reached waters with SST >4 °C, two different trip types could be distinguished for 10 out of 11 birds, and one bird was performing an alternative strategy.

Direct trips were shown by five birds (Fig. 2a); these were characterised by a straight pathway to and from one focused foraging area. While commuting and travelling in colder waters, movement

was fast and direct; on arrival in the foraging area, movements and headings showed a clear change towards more erratic movements within the limited geographic sphere of the foraging area (Fig. 3). Surface speeds also decreased while in the foraging area and increased again during travel back to the colony when birds followed their outward pathway, only in reverse (Table 1). The foraging areas of the direct trips were located either at the edge of an eddy at 49.5–50.0°S, 35.0–36.0°W (birds 02 and 16) or close to a north-eastern area of mixing where cold waters from the south meet warmer waters from the north at 50–51.5°S, 31–33.5°W (birds 15 and 17). One direct trip (bird 14) was oriented north-westward to a highly dynamic mixing area of cold waters from the east and warm waters from the west at 50–51°S, 40–41.5°W.

Circular trips were shown by five birds (Fig. 2b). They were characterised by a more constant speed over the whole trip duration (Table 1). Contrary to the direct trips, these birds did not focus their activity in one foraging area, rather they travelled along temperature gradients where different water masses mixed; their course and heading were less erratic than the movement of birds following direct trips in the foraging area. Four of the circular trip birds (birds 01, 03, 05 and 07) crossed the centre of the eddy at 50.0°S, 37.0°W where they engaged in deep foraging dives. The residence time in the eddy was only a few hours after which the birds continued heading northwards towards the strong temperature gradients between warm northern waters (>9 °C) and the colder PFZ waters close to the Falklands Ridge. One of the circular trips (bird 04) passed to the east of the eddy and the bird remained for a few days in this area but then continued north-eastwards to the PFZ boundary region. One trip (bird 06) showed characteristics of both trip types and could not clearly be assigned to one of the two trip types. This trip was excluded from further analysis (track not shown in Fig. 2).

Direct and circular trips showed no significant difference in trip duration, whereas total distance covered and maximum and mean distance to the colony were significantly greater for circular trips (Table 1).

3.2. FPT analysis and ARS behaviour

FPT variance maxima of all birds occurred at spatial scales with radius between 2 and 10 km (Fig. 4a), with different curve forms for the different trip types. Direct trips (Fig. 4b) showed single peaks in variance of $S(r) = 0.43$ and 0.47 at $r = 2$ – 4 km for birds 14 and 15, and very low variance peaks between $S(r) = 0.23$ and 0.16 at $r = 2$ – 6 km for birds 02, 16 and 17. Circular trips (Fig. 4c) had either a broader maximum of variance, $r = 2$ – 10 km, with several peaks around $S(r) = 0.7$ and 0.53 (birds 03 and 05), or a single

Table 1

Mean and standard deviation of trip type characteristics for direct and circular trips. Different trip phases are defined as: travel = 2–4 °C, search in eddy = 4–5 °C (only circular trips), foraging = >4 °C for direct trips, >5 °C for circular trips (KW: Kruskal–Wallis test).

	Direct trips (n = 5)	Circular trips (n = 5)	t-test
Trip duration (days)	20.59 ± 1.21	22.52 ± 3.38	No difference with $p = 0.26$
Total dist covered (km)	1342.66 ± 125.06	1668.74 ± 99.10	$p = 0.002$
Max dist to colony (km)	537.99 ± 46.98	709.94 ± 34.63	$p = 0.0002$
Mean dist to colony (km)	362.39 ± 56.23	470.72 ± 60.28	$p = 0.01$
			KW direct-circular
Surface speed (km/h)			
Travel to/from foraging area	3.9 ± 1.8 (n = 4470)	4.2 ± 0.9 (n = 3595)	$p = 0.016$, $F = 5.83$, $df = 8064$
Search in eddy (circular)	–	3.39 ± 1.2 (n = 1514)	–
Foraging (>4 °C direct, >5 °C circular)	2.5 ± 1.7 (n = 2434)	3.08 ± 1.3 (n = 1879)	$p < 0.001$, $F = 151.89$, $df = 4311$
KW surface speeds for different trip phases	$p < 0.001$, $F = 928$, $df = 6902$	$p < 0.001$, $F = 1170$, $df = 6985$	
Surface intervals (s)			
Travel to/from foraging area	222 ± 1788 (n = 11816)	180 ± 1121 (n = 4135)	$p < 0.001$, $F = 13.93$, $df = 15950$
Search in eddy (circular)	–	305 ± 1955 (n = 1742)	–
Foraging	323 ± 2286 (n = 6402)	350 ± 2235 (n = 2160)	$p < 0.001$, $F = 309.45$, $df = 8561$
KW surface intervals for different trip phases	$p = 0.91$, $F = 0.01$, $df = 18217$	$p < 0.001$, $F = 345.15$, $df = 8036$	

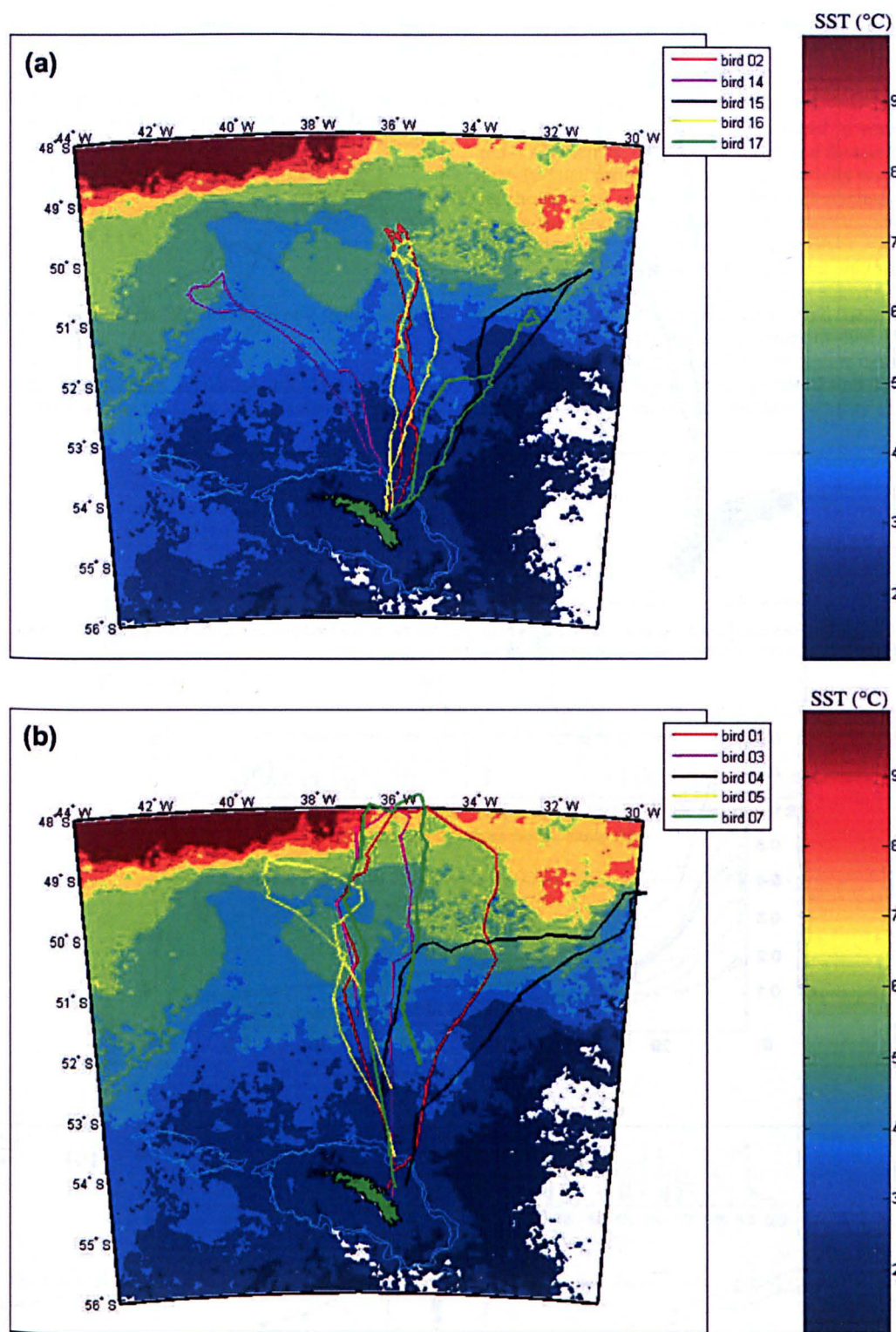


Fig. 2. Orientation of (a) direct trips and (b) circular trips, in relation to SST (SST from NOAA MODIS satellites for January 2006).

but only slowly decreasing peak in variance for birds 07, 04 and 01, with $S(r) = 0.48, 0.37$ and 0.29 . Nine out of the 10 birds studied showed a dip in $S(r)$ at $r = 12$ km; this could be further explored in the future.

The plots of FPT as a function of time since departure from the colony showed different patterns for the different trip forms for 8

out of the 10 birds. Direct trips (Fig. 5a) showed either one clear ARS hotspot with an increase and decrease of FPT (birds 02, 16 and 17) or several but clearly separated hotspots over the trip (bird 14). Circular trips (Fig. 5b) did not show a single ARS hotspot in one particular area of the trip, but several areas of elevated passage time over the whole trip (birds 01, 04, 05 and 07). Apart from bird

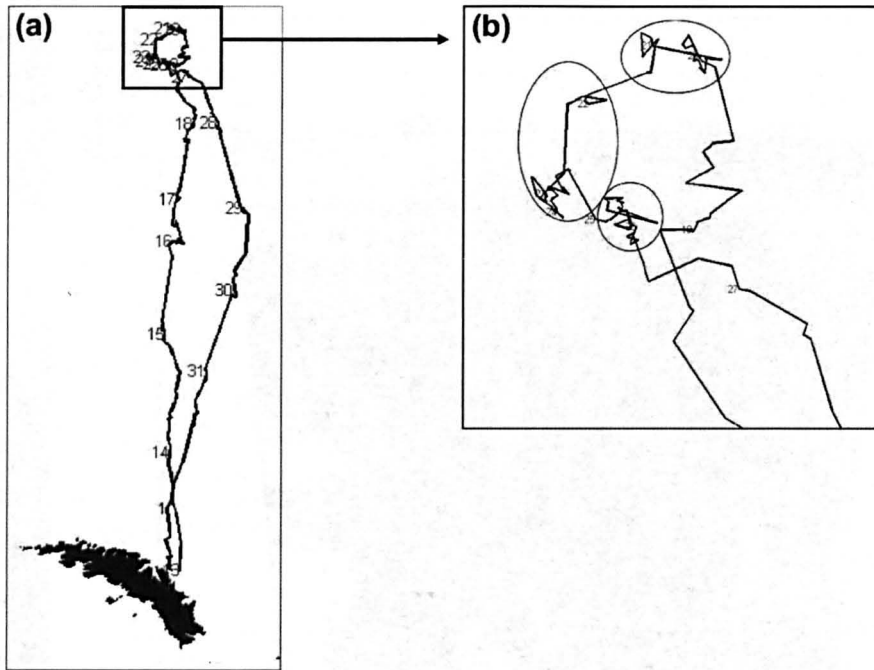


Fig. 3. Changing movements between travel and foraging phases of a direct trip (bird 16) for (a) the total trip and (b) for the foraging phase where circles indicate ARS hotspots (areas of slowest passage time). Grey numbers indicate the dates during the course of the trip.

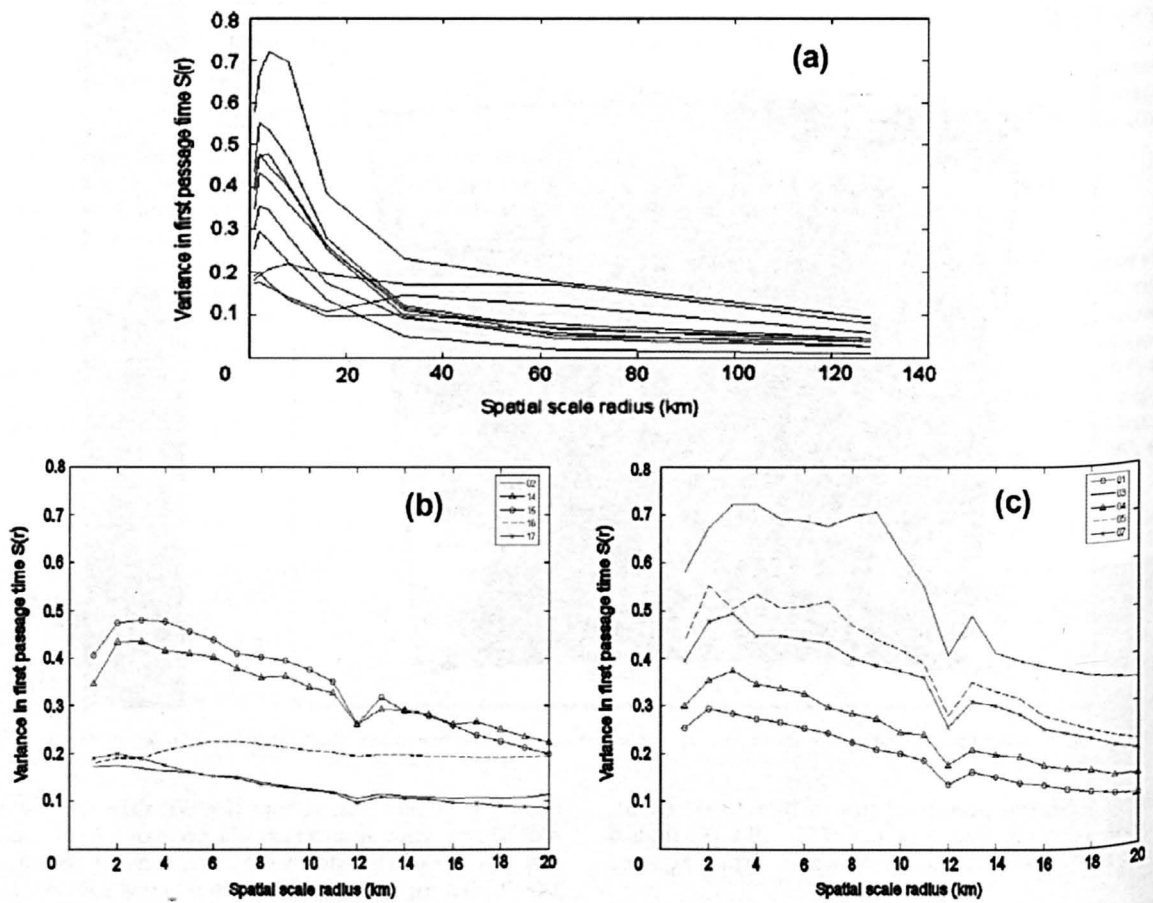


Fig. 4. Variance in first passage time $S(r)$ after Fauchald and Tveraa (2003) for (a) all trips at larger scale with $r = 1$ –128 km, (b) direct trips at finer scale with $r = 1$ –20 km, and (c) circular trips at finer scale with $r = 1$ –20 km.

03, FPT maxima for ARS hotspots from circular trips did not exceed 1 day, whereas direct trip ARS hotspots had FPT maxima between 0.7 and 2.4 days.

Two birds (birds 03 and 15) showed mixed FPT patterns even though their trip form allowed a clear assignment to circular or direct. Bird 03 showed several but clearly separated ARS hotspots over the trip with FPT maxima between 1.4 and 2.1 days for $r = 5$ km. Bird 15 showed a slow but constant increase of FPT during the first days, then a relatively constant FPT at the maximum value (never >1 day for $r = 5$ km).

3.3. Diving behaviour in relation to SST, oceanographic features, time of day and ARS behaviour

For analysis of diving behaviour we distinguished two different phases: the travel phase during the outward and inward trip in 2–

4 °C Antarctic Zone waters, and the focal foraging phase in waters >4 °C.

3.3.1. Diving behaviour in 2–4 °C Antarctic Zone waters: travel phase

Maximum diving activity was located in waters between 2 °C and 4 °C where birds executed travel and foraging dives in approximately equal proportions and diving activity was pronounced during the day and night (Fig. 6, Table 3). Foraging activity appeared during the total 24 h period, with numerous deep foraging dives during daytime and shallow foraging dives <50 m depth during night-time. Surface speeds were high, and only short surface intervals appeared (Table 1). Both trip types showed the same form of diving behaviour described above, though there were detailed differences in the exact times of maximum dive effort. Direct trips had maxima of foraging dive frequency, dive depth and dive duration during the twilight periods (Tables 2 and 3), whereas circular trips showed the maximum foraging activity during dawn with

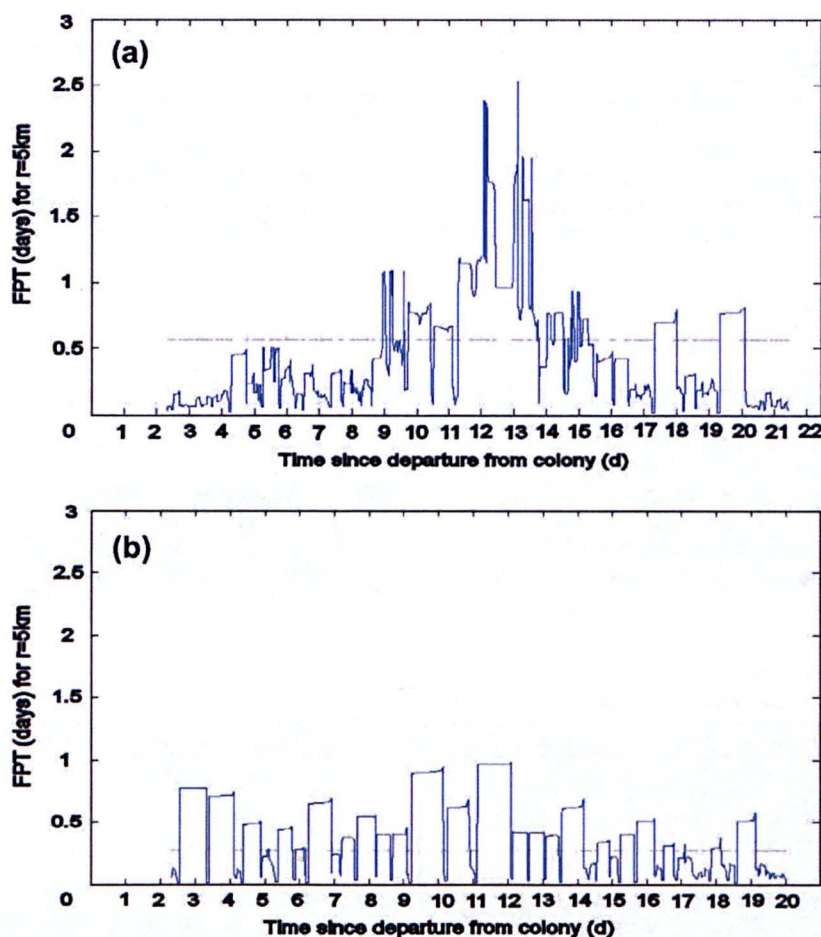


Fig. 5. First passage time for $r = 5$ km as a function of time since departure from colony for (a) a direct trip and (b) a circular trip.

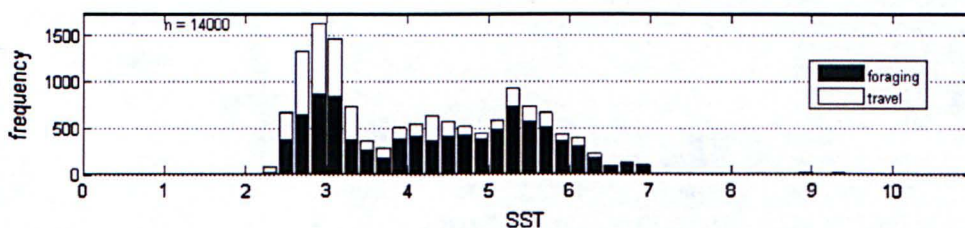


Fig. 6. Number of travel and foraging dives with increasing SST.

then a constant decrease of foraging activity over the day, but with maximal dive depth and duration around midday (Tables 2 and 3, Fig. 8a). In general, circular trips showed higher surface speeds and higher foraging activity over the total 24 h period than direct trips in 2–4 °C waters (Tables 1 and 3).

3.3.2. Diving behaviour in waters >4 °C

With the birds arrival in waters >4 °C, travel activity and surface speeds decreased and surface intervals increased (Table 1). Diving behaviour showed a more marked diurnal pattern, with far fewer travel dives and almost no foraging dives during night-time. During daytime and twilight periods, diving behaviour showed continuous foraging activity with frequency maxima in the twilight hours. Direct trip types generally showed a higher foraging activity, with the maximum during the dawn period (Table 3). With a finer resolution temperature differentiation of waters >4 °C, a clear change in diving behaviour appeared in circular trips with regards to foraging activity and several dive parameters (Tables 3 and 4a and b; Fig. 8). In 4–5 °C waters across the eddy, foraging dives frequency showed pronounced maxima during twilight periods and a minimum around midday (Table 3). Dive depth, duration and bottom activity showed clear maxima at midday (Table 4a). Surface speed decreased compared to the prior travel phase in 2–4 °C waters, but was significantly higher than surface speeds of direct trips in the same SST zone (Table 1). With the birds arrival in waters >6 °C, diving behaviour changed showing an inverse pattern of the behaviour in the eddy. Dive depth and duration as well as

bottom activity and number of reversals all showed significant ($p < 0.01$) maxima during the twilight hours and minima around midday (Table 4b). From SST >5 °C, dive depth and duration during twilight hours increased with SST (Table 5). With SST >6 °C, only a small number of records ($n = 471$) were available for analysis due to memory limitations in the TDR devices.

Foraging dive frequency within the ARS hotspots changed with latitude. At higher latitudes, foraging dives occurred within and outside of ARS hotspots, and with decreasing latitude, the foraging dives were reduced outside the ARS hotspots and increased within the ARS hotspots (Fig. 7). This behaviour was more pronounced for direct than for circular trips, especially for the two birds targeting the edge of the eddy (birds 02 and 16); these birds showed a strongly reduced foraging dive frequency in latitudes >51°S and an intense foraging activity within ARS hotspots around 50°S.

Several dive parameters showed significant differences within and outside of ARS hotspots, especially for direct trips (Table 6). Within ARS hotspots, birds executed deeper and longer dives with elevated bottom time and bottom activity, but the number of reversals did not show significant differences. Surface speed was reduced within ARS hotspots. SST values showed significant differences within and outside ARS hotspots, with a mean ARS hotspot SST of 4.11 °C and 3.24 °C in other areas. Circular trips also showed changes in diving behaviour, but not all dive parameters showed significant differences. A comparison of dive parameters within ARS hotspots between direct and circular trips did not show any significant differences (Table 6).

Table 2

Dive depth and duration over the day period in 2–4 °C waters (KW: Kruskal–Wallis test).

	Twilight ($n = 1183$)	Rest daylight period ($n = 4972$)	KW
(a) for direct trips			
Dive depth (m)	74.47 ± 69.45	53.58 ± 62.29	$p < 0.001$, $F = 158.39$
Dive duration (s)	158.98 ± 102.1	126.89 ± 104.4	$p < 0.001$, $F = 91.86$
	Midday ($n = 231$)	Rest daylight period incl. twilight ($n = 1686$)	KW
(b) for circular trips			
Dive depth (m)	76.36 ± 62.32	66.64 ± 57.24	$p < 0.001$, $F = 56.73$
Dive duration (s)	166.64 ± 113.19	156.45 ± 103.42	$p = 0$, $F = 56.72$

Table 3

Foraging activity (foraging dives/h) in different SST zones for direct (D) and circular (C) trips.

	D dawn	D dusk	D midday	D days	D nights	C dawn	C dusk	C midday	C days	C nights
Travel										
2–4 °C	7.5	5.7	4.3	4.8	4.8	9.0	5.4	6.8	6.3	7.5
Eddy										
4–5 °C	–	–	–	–	–	9.6	9.3	4.6	8.5	0.8
Forage										
>4 °C	14.6	11.3	10.3	9.2	1.9					
>6 °C						7.7	7.9	5.3	7.8	1.1

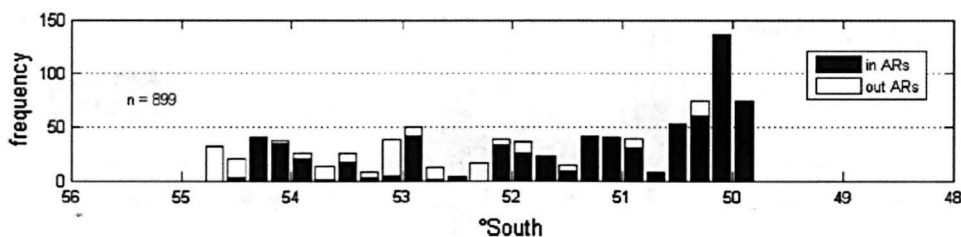


Fig. 7. Number of foraging dives within and outside of ARS hotspots as a function of latitude for a direct trip.

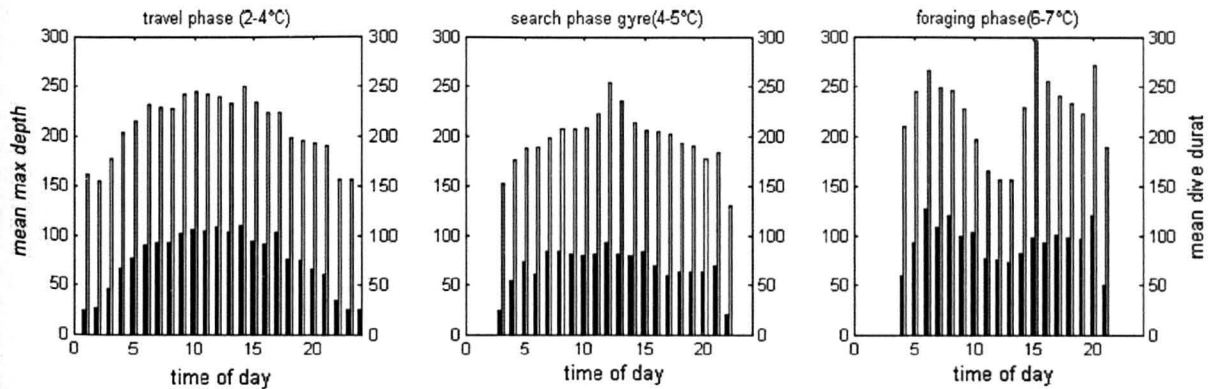


Fig. 8. Dive depth and dive duration for different SST zones for foraging dives of circular trips.

Table 4

Changing dive parameters over the day period. Values are means \pm standard deviation.

	Dawn	Dusk	Rest daylight period incl. midday	KW test ($df = 1364$)
(a) In waters of 4–5 °C for circular trips (eddy passage)				
Dive depth (m)	56.3 \pm 36.6	61.9 \pm 28.1	70.7 \pm 40.9	$p < 0.01$, $F = 26.4$
Dive duration (s)	179.2 \pm 32.9	170.2 \pm 52.8	195.1 \pm 61.1	$p < 0.01$, $F = 66.2$
Bottom activity (m)	94.81 \pm 37.25	101 \pm 31.29	108.05 \pm 38.32	$p < 0.005$, $F = 31.68$
Number of reversals	7.82 \pm 4.84	8.15 \pm 4.05	7.16 \pm 4.51	$p < 0.005$, $F = 11.45$
	Midday		Rest daylight period incl. twilight	KW test ($df = 339$)
(b) In waters >6 °C for circular trips (after eddy passage)				
Dive depth (m)	68.7 \pm 21.0		100.7 \pm 38.9	$p < 0.001$, $F = 32.5$
Dive duration (s)	145.6 \pm 41.5		222.2 \pm 62.8	$p < 0.001$, $F = 54.7$
Bottom activity	78.4 \pm 26.4		117.5 \pm 37.9	$p < 0.001$, $F = 40.3$
Number of reversals	4.4 \pm 2.4		5.8 \pm 3.3	$p < 0.001$, $F = 4.4$

Table 5

Changing dive depth and duration during twilight hours for increasing SST >5 °C for circular trips.

	Dive depth (m)	Dive duration (s)
5–6 °C ($n = 380$)	73.21 \pm 45.10	190.54 \pm 70.99
6–7 °C ($n = 76$)	97.75 \pm 37.65	239 \pm 53.88
>7 °C ($n = 14$)	120.79 \pm 15.7	232.14 \pm 25.42
KW test ($df = 469$)	$p < 0.01$, $F = 40.31$	$p < 0.01$, $F = 45.97$

4. Discussion

At South Georgia, King Penguin foraging trips showed clear associations with oceanographic features, particularly strong thermal gradients or an eddy in the PZF. Two different behaviours were

evident that resulted in two different foraging trip types. It is likely that both trip types were a direct consequence of prey encounter rates and distribution, both of which are likely to be associated with these oceanographic features. King Penguins appeared to use Area Restricted Search (ARS) in different patterns to exploit the environment depending upon conditions encountered. Variation in several dive parameters was apparent during the trips and was related to time of day, SST and ARS behaviour.

4.1. Trip orientation and ARS behaviour in relation to SST and mesoscale oceanographic features

All trips were clearly oriented northwards towards the Polar Frontal Zone and regions with SST >4 °C. The PZF is a complex, cir-

Table 6

Mean dive parameters for foraging dives for all birds of (a) direct and (b) circular trips within and outside of ARS hotspots. KW test = Kruskal Wallis test results (for $df = 8$), in = within ARS hotspots, out = outside of ARS hotspots.

	Depth		Duration		Number of reversals		Bottom activity		Bottom duration		SST		Surface speed	
	In	Out	In	Out	In	Out	In	Out	In	Out	In	Out	In	Out
(a) Direct trips ($n = 4110$)														
B02	74.66	66.26	210.75	197.37	7.61	6.45	115.12	99.68	113.12	97.68	4.19	3.32	3.53	4.19
B14	87.64	39.49	196.60	133.69	5.41	3.41	101.75	63.83	99.75	61.83	4.14	2.68	2.42	3.89
B15	103.56	62.36	229.93	184.72	5.74	6.75	116.01	97.91	114.01	95.91	3.42	3.18	3.42	3.93
B16	101.88	68.26	225.53	192	5.73	5.9	119.23	97.04	117.23	95.04	4.43	3.2	2.63	4.94
B17	118.10	94.51	236.94	223.58	5.65	5.27	120.42	111.55	118.42	109.55	2.87	2.82	2.32	3.83
KW test	$p < 0.01$		$p < 0.01$		$p = 0.92$		$p < 0.01$		$p < 0.01$		$p < 0.01$		$p < 0.01$	
(b) Circular trips ($n = 5246$)														
B01	85.18	75.07	227.01	222.98	6.59	6.41	121.64	117.46	119.64	115.46	3.99	3.72	3.99	5.05
B03	72.12	56.89	189.90	171.74	7.35	6.69	110.5	94.08	108.5	92.08	5.23	3.14	2.68	4.02
B04	85.04	80.36	213.08	204.71	7.19	5.16	111.71	93.34	109.71	91.34	4.21	2.91	3.04	3.22
B05	99.44	49.65	232.38	168.83	5.77	4.62	119.76	86.41	117.76	84.41	4.33	2.54	3.81	4.44
B07	88.11	78.06	214.11	201.21	6.65	5.34	116.92	90.17	114.92	88.17	4.28	4.36	4.12	4.04
KW test	$p < 0.01$		$p > 0.05$		$p = 0.76$		$p < 0.01$		$p < 0.01$		$p = 0.75$		$p = 0.12$	

cumpolar transition region between the Antarctic and sub-Antarctic surface waters; in places it is constrained by bathymetry where it is characterised by the presence of high-energy eddies and meanders (Gordon et al., 1977; Moore et al., 1999). Mesoscale oceanographic features related to the local bathymetry in the PFZ north of South Georgia have been reported in earlier studies (Rodhouse et al., 1996; Trathan et al., 1997), particularly for the region situated over the northern end of the North-east Georgia Rise and near to the gap in the Falkland Ridge. In this region, the warm-core eddy described in this study appears to be a recurrent and temporally stable feature.

King Penguins feed mainly on myctophid fish (Williams, 1995; Bost et al., 1997, 2002; Olsson and North, 1997; Cherel et al., 2002) and therefore their foraging strategies are likely to be strongly related to the biogeography of these prey. In the Atlantic sector of the Southern Ocean, myctophid fish are highly abundant in the frontal regions of the PFZ, though their biomass decreases farther south (Pakhomov et al., 1994). Rodhouse et al. (1996) suggest that the mesoscale distribution of myctophids may be related to frontal systems and particularly to warm-core eddies which may therefore constitute reliable foraging regions for myctophid predators. Birds in this study appeared to target regions in the PFZ where they had a high probability of encountering mesoscale oceanographic features that provide zones of elevated biological productivity (Thomas and Emery, 1988) and a high probability of prey encounter with the best foraging success in terms of CPUE (catch per unit effort) despite the remoteness of this foraging area. The importance of warm-core eddies as foraging regions for King Penguins is certainly supported by 8 of the 11 birds tracked in this study, as their initial foraging focus coincided with the mesoscale eddy described above or regions close to its eastern edge.

Direct trips concentrated on one limited foraging area after the direct outwards travel period, presumably as a consequence of a successful search for dense and stable prey patches in the first region explored. Regions with adequate prey resources to allow this foraging strategy were located at the edge of certain mesoscale oceanographic features; either the warm-core eddy in the PFZ or the strong thermal gradients within or on the limits of the PFZ. Such precisely oriented foraging to the edge of eddies has been reported for Grey-headed Albatrosses (*Thalassarche chrysostoma*) in the Southern Indian Ocean (Nel et al., 2001) and at South Georgia (Rodhouse et al., 1996). Birds targeting one very limited foraging area (birds 02, 16 and 17) showed a similar FPT pattern, with one clear ARS hotspot between the outwards and inwards travel period and a low first passage time (FPT) variance peak. This could be the result of a direct encounter with dense prey aggregations in the border region of the eddy due to small-scale oceanographic features in this boundary that would only require a low search effort in a very limited area. Direct trips with a search effort over a broader area (birds 14 and 15) showed several ARS hotspots and higher peaks in FPT variance. This could be the result of dense but more dispersed prey patches in the foraging area, which enabled birds to execute ARS on small scales once a prey patch was found, but meant birds subsequently needed to locate other prey patches. The high FPT variance peak indicates that search effort had to be more intense than that during the three other direct trips with only one ARS hotspot. Bird 14 foraged towards the north-west of the study area where colder, fresher waters from the Scotia Sea originating southeast of South Georgia mixed with warmer, more saline waters originating from the Scotia Sea west of South Georgia (Trathan et al., 1997). This results in a highly dynamic area with small-scale oceanographic features and strong temporal and spatial variability (Trathan et al., 1997), which is likely to support high biological productivity over an extended area. The meander in the foraging pathway at the north-western end of this trip and several ARS hotspots over the course of the trip could indicate that possi-

bly spatially and temporally less stable prey were associated with small-scale oceanographic features (Fauchald et al., 2000) over the entire area.

Circular trips with travel along temperature gradients were potentially the result of the encounter of prey resources that were insufficient for efficient foraging in the first regions targeted within the PFZ. Trip form and various ARS hotspots over the whole trip duration with lower maximum passage times than for direct trips indicate that these birds had to search constantly for prey while moving along temperature gradients. The differences in FPT variance maximum values and spatial scales may indicate that birds utilised different search efforts at different scales for prey detection: a larger-scale search to locate prey patches along their pathway, and a search effort at a smaller scale in a restricted area once a dense prey patch was found. Four birds showed a direct northwards trajectory towards the warm-core eddy in the PFZ crossing the eddy at its centre. Within the eddy the conditions may not be favourable for efficient foraging (see Section 4.2) and birds continued heading towards regions of strong temperature gradients after several hours.

Some of the birds showed characteristics of both trip types in either trip form or FPT pattern. There were two main obvious trip forms with direct and circular trips identifiable with the quantity and resolution of our data; however, it is possible that behaviour can show intermediate forms, presumably as a consequence of spontaneous individual adaptations to conditions encountered during the trip. Due to the resolution of our ARGOS data, behaviour at scales of less than 15 km was smoothed (see Trathan et al., 2008). ARS in this study appeared at scales of $r = 2\text{--}10$ km, which makes statements about search behaviour of tracked birds at scales less than this, speculative. In this study, we highlight some behavioural tendencies of King Penguin foraging strategy, but more precise tracking data with GPS loggers (see Trathan et al., 2008) and data on feeding activity are needed to get more detailed insights into King Penguin foraging behaviour and to identify more precisely the feeding regions and correlations with environmental conditions.

Circular trips had a significantly greater foraging range and reached more distant waters than direct trips, whereas there was no significant difference in trip duration (Table 1). This implies greater surface speeds over the whole trip (Table 1), which could result in the need for higher prey ingestion rates to compensate for the higher energy costs associated with travelling (Froget et al., 2004). It is plausible that the favoured foraging strategy would target the nearest foraging areas in order to minimise energetic costs, but that birds must modify this strategy in response to conditions encountered, even though such a modification may be less efficient in terms of energy costs.

Changes in the patterns of movement from a direct heading while travelling to a more erratic movement in the foraging area, may be related to the rate of encounter of prey patches and increased search effort in a restricted area at a small scale (Fauchald, 1999). Such behaviour has already been reported for foraging albatrosses (Weimerskirch et al., 1997; Weimerskirch, 2007; Pinaud and Weimerskirch, 2005), murre and petrels (Fauchald et al., 2000; Fauchald and Tveraa, 2003), and corresponds to theoretical predictions of animal movements during foraging in heterogeneous environments (Fauchald, 1999). This change in behaviour is particularly obvious between the travel and foraging phases in direct trips. However, it is also plausible that similar changes in behaviour occur on circular trips as has been reported for foraging albatrosses (Weimerskirch, 2007), but due to the scale of available ARGOS data, the smaller-scale foraging hotspots were not detectable. Weimerskirch (2007) describes analogous behaviour with two different trip types for foraging albatrosses, but with a much higher proportion of direct trips than circular trips (93% direct).

This may be due to the lower travelling speed of penguins (Lovvorn and Liggins, 2002) compared to flying seabirds that may allow flying seabirds to explore a much greater foraging area for a direct trip type than penguins. Therefore, penguins may be highly dependent on smaller-scale oceanographic structures that are less stable and predictable in temporal and spatial terms (Fauchald et al., 2000), which may explain the lower percentage of direct trips in penguins foraging behaviour compared to flying seabirds.

It has already been suggested that King Penguins have alternative foraging strategies in relation to the sea surface temperature and that frontal zones play a major role in the non-random exploitation of the oceanographic habitat by King Penguins (Bost et al., 1997; Guinet et al., 1997; Charrassin and Bost, 2001; Cotté et al., 2007) and other seabirds (Hull et al., 1997; Weimerskirch, 2007). Factors determining their trip orientation remain unclear. Other studies have already shown that the breeding status of birds affects their trip duration (Guinet et al., 1997) and trip type (Jouventin et al., 1994; Hull et al., 1997; Nel et al., 2001). Guinet et al. (1997) reported that incubating King Penguins did not necessarily travel as far as they could, but rather remained in areas with SST of 4–5 °C, which may correspond to the direct trips found in this study. Hull et al. (1997) distinguished two trip types for Royal Penguins (*Eudyptes schlegeli*) foraging from Macquarie Island: direct trips were associated with predictable marine resources, circular trips with feeding on less predictable and patchy resources. Jouventin et al. (1994) distinguished two trip types for King Penguins foraging from the Crozet Islands: long direct trips were associated with predictable marine resources in the Polar Frontal Zone, and shorter circular trips with feeding on less predictable and patchy resources. However, these latter trips were for birds with hatched chicks. At South Georgia, birds also undertake such shorter trips after eggs hatch (Trathan, pers. obs.). The results of the current study correspond to direct trips exploiting more predictable resources as described by Jouventin et al. (1994) but in this study the trips were not confounded by breeding status, rather they are the result of individual adaptations to oceanographic conditions and prey distribution encountered during the trip.

All trips except one direct trip were undertaken in a clockwise direction; this pattern is particularly obvious in the circular trips that follow the currents to the east of the eddy and then the westwards current between 48°S and 49°S along the frontal zones on the northern limits of the PFZ (Trathan et al., 1997). This may indicate that birds are able to use oceanographic currents for more economic travelling, which has already been proposed for other species (Randall et al., 1981; Hull et al., 1997) and King Penguins in the southern Indian Ocean (Cotté et al., 2007). Furthermore, this behaviour confirms the predictability of oceanographic features as well as the predictability of potential prey in specific areas targeted by birds using the currents.

4.2. Diving behaviour in relation to SST, oceanographic features and time of day, and correlation with ARS behaviour

Diving behaviour showed a clear relationship with both changing water temperature and time of day. In general, birds showed a marked diurnal diving pattern, supporting previous reports from studies on King Penguins at other breeding sites (Pütz et al., 1998; Pütz and Cherel, 2005; Bost et al., 2002). Changes in SST and the presence of oceanographic features had an important influence on variation in this diurnal pattern. This is probably a reflection of adaptations in diving behaviour to different prey types and prey distributions associated with these oceanographic features. Furthermore there was a correlation between search behaviour and first passage time with diving behaviour. This study therefore highlights the correlation of general and specific changes in diving behaviour with time of day, SST and the encounter of oceanographic features as well as the correlations of search and diving behaviour.

graphic features as well as the correlations of search and diving behaviour.

4.2.1. Travel phase in 2–4 °C waters

All birds showed a direct and constant course heading while in the 2–4 °C Antarctic Zone waters south of the PFZ. Birds travelling between the colony and their preferred foraging regions in the PFZ needed to provide maximal food ingestion, which resulted in intense travel and foraging activity over the entire 24 h period, with elevated surface speeds and only short surface intervals for physiological recovery (Kooyman and Ponganis, 1990). During the night, foraging dives never exceeded 50-m depth and foraging activity was reduced compared to daylight and twilight periods. Several studies have suggested that the much reduced foraging activity with decreased dive depth and duration during night-time could be a result of the fact that visually guided King Penguins mostly fail to detect and catch prey at night due to insufficient light levels (Wilson et al., 1993; Pütz et al., 1998; Bost et al., 2002) and the increased dispersal of myctophid fish during night (Perissinotto and McQuaid, 1992; Pakhomov et al., 1996). In the cold 2–4 °C Antarctic Zone waters however, it may be that birds must dive under these suboptimal foraging conditions at night-time to provide maximal food ingestion after the long starvation period on land prior to egg laying (Williams, 1995) when foraging during the day was not sufficient, either because of higher energy needs or because prey distributions were not adequate to support exclusive daylight foraging.

The main foraging activity of all birds was during the daylight period, though diving behaviour showed some differences between direct and circular trips. High foraging activity during daylight hours has already been reported in other studies (Pütz et al., 1998; Pütz and Cherel, 2005) and is potentially associated with the fact that the maximal ambient light level around midday allows the birds to detect their prey at even greater depths. In waters of 2–4 °C, direct trips showed maximum foraging dive activity, dive depth and dive duration during the twilight hours, which may indicate that these birds did not follow their prey until its maximum depth around midday, but could concentrate their foraging effort during twilight hours when prey is more available due to its vertical migration (Pütz et al., 1998; Bost et al., 2002). In circular trips, the maximum dive depth and dive duration around midday indicates that prey was followed until its maximum depth. Some of the observed differences in diving behaviour between direct and circular trips in 2–4 °C waters could be due to the fact that TDR recordings for circular trips were only available for the outward paths and not for the return journey to the colony, whereas most direct trips (all except one) had complete TDR recordings over the entire trip. It may be that different foraging behaviour occurs on outward and return journeys, with higher surface speed, generally higher foraging activity and prey pursuit to maximum depths at midday on the outwards journey as a result of the high energy needs and demands for prey after the colony leave. On return journeys, prey ingestion may occur only to maximise energy resources and provide for chick provisioning, therefore foraging behaviour could potentially be more selective and focus on more favourable foraging periods during twilight and periods of vertical migration of prey (Pütz et al., 1998; Bost et al., 2002).

4.2.2. Foraging phase in waters >4 °C

In waters of 4–5 °C, birds reduced their intense travel activity and appeared to search for dense prey patches located close to the mesoscale features encountered in these areas. Depending on the foraging success within a given time period, birds may continue in a direct or circular trip. Conditions for dense and spatially stable prey patches may be encountered on the outside of eddies (Nel et al., 2001). Direct trips targeting such areas may be able to

exploit these prey patches and stay in the same area during the whole foraging phase. Surface speeds decreased when birds were mainly undertaking foraging dives; travelling dives potentially were only undertaken to move between small-scale features in this mesoscale area or to follow movements of prey patches (Fauchald, 1999). Due to the apparent stability and density of some patches, birds could focus their foraging on the dawn period when prey was most accessible (Bost et al., 2002). In terms of optimal foraging periods during the day and minimal energy costs due to travel and search, direct trips would seem to be an optimal foraging strategy for King Penguins in this area.

In waters of 4–5 °C, birds on a circular trip passed across the centre of the eddy. Given the elevated SST in the eddy, thermoclines would be inclined downwards and would increase the preferred depth of the targeted prey (Brandt, 1981; Glorioso et al., 2005). Maximum dive depth and duration around midday indicated that prey was targeted over the whole day and followed to its maximum depths. This behaviour is potentially a result of prey patches that may not be sufficiently dense or spatially stable to enable maximal foraging effort during twilight hours when prey is located at shallower depths (Pütz et al., 1998; Bost et al., 2002), or of fish communities in the eddy that differ from communities encountered on the edges (Brandt, 1981, 1983). Foraging on these prey is potentially too difficult or not efficient enough to focus effort in this area. Thus, birds only spent a short time undertaking this intense foraging behaviour within the eddy. Diving behaviour in the middle of the eddy showed significant differences to diving in areas outside of the eddy, but horizontal movements of the animals did not show elevated FPT and increased search effort. This could indicate that King Penguins would rather use vertical movements for prey patch detection than horizontal movements. Once a prey patch is located, diving behaviour as well as horizontal surface movement alters in order to exploit the prey source in the most efficient manner. When birds were unable to encounter favourable conditions for efficient and precisely oriented foraging in waters of 4–5 °C, they continued heading towards regions of strong temperature gradients on the northern limit of the PFZ, where prey patches may be more frequent (Thomas and Emery, 1988). Unfortunately, our TDR recording stopped for all circular trips shortly after having reached these zones of strong temperature gradient. As a result, we have only a few observations on diving behaviour in these waters. All recorded dives showed a strong bimodal distribution for dive frequency, dive depth and dive duration, which indicated a clear concentration of foraging activity at the twilight periods. Twilight dives were deeper and longer in duration in waters >6 °C and may be the result of following prey into their preferential temperature envelope to deeper waters. This may be particularly the case due to increases in the upper water column where warmer northern waters flow above PFZ waters (Gordon et al., 1977; Arhan et al., 2002). Prey are outside of the diving range when myctophids reach their deepest point at midday therefore foraging has to be concentrated in twilight hours. Despite this restriction, prey patches appear to be concentrated and sufficiently stable so as to provide adequate resources for King Penguins. However, there are only a few of records for these high SST areas and it is not possible to draw extensive conclusions on the birds behaviour.

The number of reversals may be an indicator of the intensity of foraging activity, especially if it is combined with a strong prey search activity in the water column (Simeone and Wilson, 2003; Takahashi et al., 2004). A large number of reversals during one dive allows an intense exploration of the water column with a higher chance of prey detection due to the greater volume of water searched. Bost et al. (2007) suggested a strong relationship between the number of ingested prey and the number of reversals during one dive where King Penguins were feeding on fast-moving

prey, which makes the number of reversals an appropriate indicator for feeding activity. In this study, the number of reversals showed maxima in the twilight periods (Table 4), which may indicate an intense prey search and foraging activity in this period, and confirms the importance of twilight hours for foraging. Alternatively, the elevated number of reversals may constitute a response to a more dispersed prey field during twilight hours, and thus more movements are necessary to catch dispersed prey. This has already been suggested by Pütz and Cherel (2005) with an association of W-dives (undulations occurring during the bottom period) with foraging on dispersed prey in twilight hours. More focused maxima in direct trips may confirm the hypothesis that this trip type allows a more concentrated foraging activity on twilight hours when prey is more accessible; in circular trips, a longer search effort is necessary to detect more dispersed and less stable prey patches.

The number of foraging dives executed within ARS hotspots increased with decreasing latitude and shows its maximum in waters between 50°S and 52°S, which corresponds to the geographical position of the PFZ. At the same time the foraging dives executed outside of ARS hotspots decreased strongly in these areas. This may indicate a more focused foraging behaviour within the PFZ waters, with an adjustment of horizontal and vertical foraging effort to exploit the environment in a more efficient way. This pattern is particularly pronounced for direct trips, which may indicate that these birds could undertake a focused foraging effort on a limited area. Differences in dive parameters within and outside ARS hotspots indicate a change of diving behaviour with a change in surface movements. This is especially obvious for birds undertaking direct trips when changing from travelling to foraging behaviour. All dive parameters, except the number of reversals, showed significant differences for direct trips. Deeper and longer foraging dives within the ARS hotspots with high values for bottom duration and bottom activity may reflect intense foraging activity in these areas. Pütz et al. (2006) suggest that longer bottom times may be the result of more predictable prey distributions at greater depths, which appears to coincide with our results of the diving behaviour within ARS hotspots. Higher bottom activity but no significant change in the number of reversals may indicate foraging on more concentrated prey patches with less reversals needed for prey capture.

5. Conclusion

The importance of the PFZ as a key foraging area for King Penguins and other marine predators has been recognised in earlier studies in the Southern Indian Ocean (Jouventin et al., 1994; Bost et al., 1997; Guinet et al., 1997; Hull et al., 1997; Pütz et al., 1998; Charrassin and Bost, 2001; Bailleul et al., 2007). This study confirms the importance of this oceanographic area for King Penguins breeding at South Georgia. Here, oceanographic features such as frontal systems and eddies also appear to play an important role in the foraging behaviour of these marine predators as it does in the southern Indian Ocean (Nel et al., 2001; Côté et al., 2007). It is probable that King Penguins concentrate their foraging search activity in parts of the ocean where oceanographic features provide predictable feeding resources. In order to exploit the marine environment in an optimal way, King Penguins seem to use area restricted search and adjust their foraging behaviour upon conditions encountered. To gain greater insights into the finer-scale foraging behaviour, higher resolution tracking data as well as feeding data are needed.

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Frontal zones, temperature gradient and depth characterize the foraging habitat of king penguins at South Georgia

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ABSTRACT: Investigating the responses of marine predators to oceanographic structures is of key importance for understanding their foraging behaviour and reproductive success. Using Global Positioning System (GPS) and Time-Depth-Temperature-Recorder (TDR) tags, we investigated how king penguins breeding at South Georgia explore their foraging area over the summer season in both the horizontal and vertical dimensions. We determined how horizontal habitat use may relate to different Antarctic Circumpolar Current (ACC) frontal zones and associated thermal structuring of the water column. To study the penguins' use of the water column, we examined foraging niches defined by temperature, temperature gradient and depth, and explored the importance of these thermal properties for prey pursuit. King penguins foraged within the Polar Front (PF) and its southern edges during incubation, and the Antarctic Zone (AAZ) and Southern ACC Front (SACCF) during brooding. Foraging niches became more distinct with the advancing summer season, defined by strong thermal gradients at shallow depths in the AAZ, and weak gradients at greater depths in the SACCF. These niches indicate foraging in the sub-thermocline Winter Water (WW) in the AAZ, and in deep WW and Circumpolar Deep Water (CDW) at the SACCF. The influence of different ACC frontal zones in the area to the north of South Georgia appears to provide for a horizontally and vertically segregated environment. The presence of optional foraging areas and niches close to the colony clearly play an important role in these king penguins' foraging success.

KEY WORDS: *Aptenodytes patagonicus* · Hydrological structure · Antarctic Circumpolar Current · Temperature gradient · Foraging niche · Seabird

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INTRODUCTION

The behaviour and distribution of marine predators are generally thought to be determined by the location of their prey, but influenced by specific time and energy constraints. Prey distribution is strongly influenced by the structure of the marine environment (Owen 1981, Franks 1992), which is determined by physical properties such as temperature and temperature gradient. They govern the concentration of nutrients in the water column (Lima et al. 2002), which in turn influence the distribution and abun-

dance of planktonic organisms and, hence, higher trophic levels including the prey of apex predators (Owen 1981, Lutjeharms 1985, Schneider 1990). Surface features such as oceanographic fronts arise from where different water masses meet (Schneider 1990), and are, therefore, locations where different habitats as well as strong physical gradients occur in a spatially restricted area. Such a heterogeneous environment may be crucial for the existence of distinct foraging niches for predators.

King penguins are one of the most important avian consumers in the Southern Ocean (Woehler 1995).

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They feed mainly on myctophids (Cherel & Ridoux 1992, Olsson & North 1997), mesopelagic fish that are generally associated with particular water masses or temperature ranges (Hulley 1981, Kozlov et al. 1991, Collins et al. 2012, Fielding et al. 2012), as well as with fronts and related oceanographic features (Brandt et al. 1981, Kozlov et al. 1991, Pakhomov et al. 1996, Rodhouse et al. 1996). Among diving birds, king penguins are able to forage at depths of over 300 m (Charrassin et al. 2002), and are known to use thermal discontinuities for foraging (Charrassin & Bost 2001). However, we still have little detailed understanding about how these predators may explore the thermal structure of the water column in different marine environments, and how habitat use may be adjusted depending upon changing constraints.

King penguins experience changing time and energy constraints over the summer breeding season (Charrassin et al. 2002, Halsey et al. 2010). During incubation (December to February), each parent alternately incubates and then returns to sea to restore its body reserves in 2 to 3 wk long foraging trips (Bost et al. 1997). After hatching, chick rearing (February to March) causes increased energy demand since the chick must be provisioned regularly (Charrassin et al. 1998). It is likely that changes in foraging behaviour reflect how these predators access the most profitable oceanographic structures according to their time and energy constraints. In this context, the thermal structuring of the foraging area and the presence of different foraging niches may play an important role (Charrassin & Bost 2001).

South Georgia is situated within the Antarctic Circumpolar Current (ACC), the most pronounced feature of the Southern Ocean circulation (Rintoul et al. 2001). It includes 3 major deep-reaching fronts, from north to south, the SubAntarctic Front (SAF), the Polar Front (PF) and the southern ACC Front (SACCF) (Orsi et al. 1995). The PF is an important foraging area for incubating king penguins at South Georgia (Trathan et al. 2008, Scheffer et al. 2010). However, there is no information on how changing breeding constraints may affect foraging behaviour, and how this may relate to local oceanography. For king penguins, foraging areas close to the SACCF have not yet been considered, despite the key role of this front for the Scotia Sea ecosystem (Thorpe et al. 2002, 2004, Ward et al. 2002, Murphy et al. 2004) and its close proximity to the breeding colonies at South Georgia. We know very little about features in the vertical dimension that may restrict efficient foraging for diving predators such as king penguins, or how this may relate to any changing constraints for these

birds. Identifying such features and their association with different oceanographic areas may increase our understanding of how horizontal habitat use by diving predators is related to their exploration of the water column. This may be of importance in the context of environmental change, and any future potential effects on king penguin populations (Le Bohec et al. 2008, Forcada & Trathan 2009, Péron et al. 2012).

We investigated how king penguins breeding at South Georgia explore their available foraging area over the summer season in the horizontal and vertical dimensions. Using a combination of Global Positioning System (GPS) tracking and time-depth-temperature recorders (TDR), we addressed the question of how horizontal habitat use may relate to different ACC frontal zones and associated thermal structuring of the water column, and how diving behaviour, presumably targeting particular niches in the water column, changed accordingly. The results are discussed in the context of environmental variability and the potential vulnerability of diving predators such as king penguins to future environmental change.

MATERIALS AND METHODS

Study area, study period and device deployments

The study was conducted at the Hound Bay king penguin breeding colony on the northeast coast of South Georgia (54.23° S, 36.15° W) during the austral summers of 2005 to 2006 and 2006 to 2007. In total, 17 adult breeding king penguins were tagged: (1) during incubation in December 2005 to January 2006 (Early Incubation, $n = 4$, female), (2) during late incubation in January to February 2007 (Late Incubation, $n = 4$, unknown sex) and (3) during brooding ($n = 9$, unknown sex). Brooding birds were subsequently distinguished into Brooding I and Brooding II based on behaviour (see 'Results').

The horizontal movements of penguins were tracked by Track-Tag GPS loggers (Navsys; further details of Track-Tag are available at www.navsys.com/Products/tracktag.htm), which require only 60 ms to store raw GPS data. Devices were programmed to record positions at 60 s intervals and were equipped with a saltwater switch to delay acquisition while birds were under water. Loggers, with batteries and housing, weighed 55 g (<0.5% of body mass) and measured 35 × 100 × 15 mm (<0.7% of the cross sectional area of the body). Diving behaviour was recorded by TDR (Wildlife Computers). TDR devices

were programmed to record depth and water temperature at 1 s intervals when wet. Recordings during surface periods were halted by a saltwater switch and resumed when the bird restarted diving. The resolution of depth recordings was 0.5 m. TDRs weighed 30 g ($<0.25\%$ of body mass) and measured $15 \times 100 \times 15$ mm (Mk9) and $10 \times 90 \times 20$ mm (Mk7) ($<0.5\%$ of the cross sectional area of the body). Of the 17 penguins equipped with GPS devices, 13 of them had Mk9 TDR with external fast-responding temperature sensors, 2 had Mk7 TDR and 2 were without TDR devices. Devices were attached using methods modified from Wilson et al. 1997. All devices were recovered after a single foraging trip (varying between 5 and 23 d). In 2007, all tracked birds were weighed before leaving for sea and after their return to land to determine body mass gain during the foraging trips.

Oceanography of the study area

South Georgia is a sub-Antarctic island situated within the path of the ACC, with the PF to the north and the SACCF close to the island (Fig. 1). In contrast to most other king penguin breeding colonies which are located north of the PF (Bost et al. 2009), South Georgia is situated south of the PF. The PF is commonly defined as the location where cold Antarctic subsurface waters sink below warmer sub-Antarctic

waters (Deacon 1933), corresponding to the northernmost extent of the subsurface temperature minimum, $<2^\circ\text{C}$ near 200 m depth (Belkin & Gordon 1996). The flow regime close to South Georgia is dominated by the SACCF, which loops anticyclonically around the South Georgia peri-insular shelf before retroflecting north of the island (Orsi et al. 1995, Thorpe et al. 2002, Meredith et al. 2003) at $\sim 36^\circ\text{W}$. The SACCF flow is rich in nutrients (Ward et al. 2002), and hosts high biomass of zooplankton (Murphy et al. 2004). The Antarctic Zone (AAZ) is situated between the PF and the SACCF; it is characterized by the meeting of cold Antarctic waters and warmer surface waters from the PF. A complex eddy field has been described in the AAZ north of South Georgia as well as a warm-core anticyclonic circulation at around 52°S , 35°W (Meredith et al. 2003). Recent definitions of ACC fronts and zones in terms of Sea Surface Height (SSH) allow the identification of such features from altimetry data (Sokolov & Rintoul 2009, Venables et al. 2012), and the assignation of specific thermal profiles to frontal zones (Venables et al. 2012). In the Scotia Sea, the vertical structure of the water column includes the Surface Mixed Layer (SML), and the underlying cold Winter Waters (WW) originating from the previous winter mixed layer. The SML and WW are separated by a thermocline, a strong vertical temperature gradient of variable extent and intensity. Below the WW layer (from ~ 250 to 300 m), temperatures rise towards 2°C , characterizing the Circumpolar Deep Water (CDW).

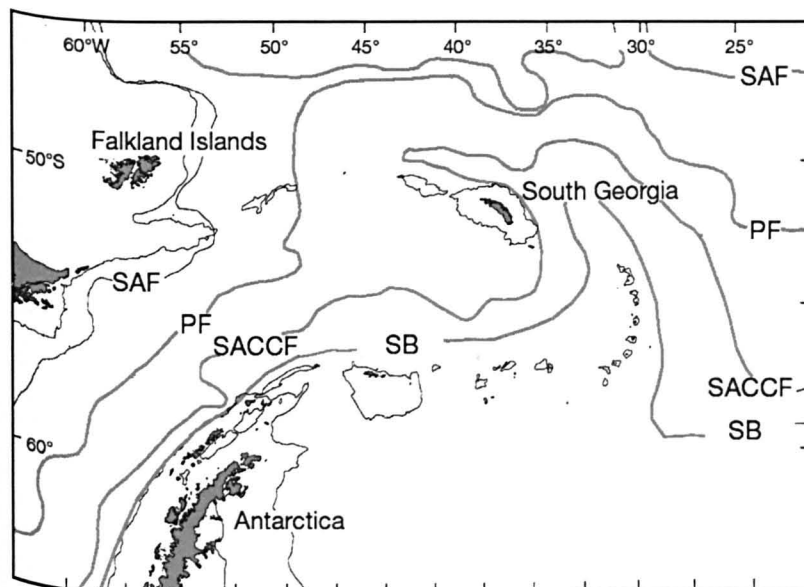


Fig. 1. South Georgia and the Antarctic Circumpolar Current (ACC) frontal positions in the Scotia Sea. Fronts: thick grey lines; 500 m and 1000 m isobaths: dark grey. Frontal positions from Orsi et al. (1995). SAF: Sub-Antarctic Front; PF: Polar Front; SACCF: Southern ACC Front; SB: Southern ACC Boundary

Oceanographic data

SSH data

Changes in SSH encountered by the penguins over their foraging trips were analyzed using Aviso (www.aviso.oceanobs.com) absolute dynamic topography (ADT) data. We used Near-real time (NRT) data available at a higher temporal resolution than the delayed time (DT) products. Data were available at a spatial resolution of $1/3^\circ \times 1/3^\circ$ and a biweekly temporal resolution. SSH values at each dive location were estimated by searching for the geographically nearest value within the corresponding dataset.

Vertical temperature data

Vertical temperature values were obtained from the external Mk9 sensor data after applying appropriate temperature correction factors from the device calibration data sheets (Wildlife Computers). Mk7 temperature data were not used due to long response times of the internal temperature sensors. Mk9 temperature sensors provide high quality data (accuracy $0.1^{\circ}\text{C} \pm 0.05^{\circ}\text{C}$, Simmons et al. 2009), and were, therefore, used for determining the properties of the water column encountered during the penguins' dives. To compensate for the surface heating effect by direct sun exposure and penguin body temperature on the temperature sensors (McCafferty et al. 2007), temperature values collected between 0 and 10 m were replaced by the value measured at 10 m depth during the ascent. The vertical water temperature gradient for each recorded depth point was also calculated; this was estimated as the temperature difference between 25 m above and 25 m below the given depth point. Temperature gradients near to the depth extremes of a dive were calculated using the maximal depth range possible (limited by the surface for points <25 m depth, and by the maximal dive depth for points >max. depth 25 m). The resulting possible bias in gradient values may only affect the depth range between the maximum depth range of a dive and 25 m above, as dives <50 m were not considered for analyses of foraging behaviour (see Data analysis). A temperature gradient of 1 thus corresponds to a temperature increase of 1°C per 50 m depth, -1 to a temperature decrease of 1°C per 50 m.

Data analysis

Data analyses were performed using Matlab (MathWorks) and the custom-made software Multi-Trace (Jensen software systems).

Analysis of surface and diving behaviour

GPS data were filtered to remove positions with navigation class >2, where class categories were 0: good, 1: altitude aided, 2: marginal position dilution of precision, and 3: bad. For each bird, we calculated trip duration, distance covered, max. distance from the colony and the furthest latitude south reached. Exact departure and return times from and to the island were determined from the TDR data. A foraging zone coefficient (FZC) was calculated as the total

trip length (km) divided by the max. distance from the colony (km) (modified from Guinet et al. 1997, Hull et al. 1997), indicating the degree of directness or looping of a foraging trip.

A zero offset correction was applied on the dive data. Only dives >50 m depth were used for analysis, as they were considered to represent the majority of king penguins foraging dives (Pütz et al. 1998, Charassin et al. 2002). Diving behaviour was analysed by calculating the following dive parameters: dive depth, dive duration, bottom duration (the time between the first and last wiggle or dive step deeper than 75% of the maximum dive depth, following Halsey et al. 2007), the number of wiggles (deviations >1 m of depth with an absolute vertical instant >0) as a proxy of feeding success (Bost et al. 2007) and broadness index (bottom duration:dive duration, indicating the proportion of a dive used for the bottom period, see Halsey et al. 2007 for more details). Furthermore, we determined the total vertical distance travelled per day, the dive frequency, the percentage of submerged time compared to the total time at sea, and the percentage of submerged time spent at depths >150 m as proxies of foraging effort. As king penguins are visual feeders and essentially forage during the daylight and twilight hours (Bost et al. 2002), night dives were excluded from the analyses. Exact sunrise and sunset times were calculated as described in Scheffer et al. 2010. Geographical coordinates at the start of each dive were interpolated based on time from the GPS data, assuming straight line travel and constant speed between 2 location points (Weavers 1992).

Principal Component Analysis (PCA) was carried out on 15 variables characterizing foraging behaviour (surface movements and diving behaviour, see Table 1 for the complete listing of all PCA variables), allowing identification of the main variables accounting for differences in foraging behaviour as well as behavioural groupings of birds. Dive parameters among grouped birds were compared using Kruskal-Wallis statistics as tests for normality failed (Jarque Bera test) and transformations did not help the data to conform to the normality assumption. When significant differences were found among groups, an all pairwise multiple comparison (Dunn's method) was performed to determine the groups that differed from the others.

Analysis of horizontal and vertical habitat use

The horizontal habitat use of king penguins was analysed with respect to trip orientation relative to

Table 1. Principal component analysis of the foraging parameters. Component loadings of the different variables

Variable	PC1 (75.7%)	PC2 (21.8%)
Dive depth	0.1717	0.1133
Dive duration	0.0551	0.0456
Bottom duration	-0.0868	-0.2066
No. wiggles/dive	-0.0613	-0.3846
Dive frequency	-0.0812	-0.2237
% time submerged	0.0498	-0.0957
% time submerged >150 m	0.5444	0.3738
No. wiggles:time submerged	-0.0718	-0.5024
No. wiggles:bottom duration	0.0217	-0.1862
Depth range index	-0.0336	-0.1832
Broadness index	-0.1306	-0.2522
Vertical distance:day	0.1422	-0.0198
Trip duration	-0.4662	0.3432
Trip length	-0.487	0.2627
Max. distance from colony	-0.3902	0.1557

the different ACC fronts. The ACC fronts and zones were defined based on SSH signatures following Venables et al. (2012). The penguin's vertical habitat use was analysed with respect to the exploration of depth and thermal properties of the water column relative to the ACC fronts. We considered the bottom phases of dives, which is thought to be the most important phase for prey capture (Charrassin et al. 2002, Simeone & Wilson 2003, Ropert-Coudert et al. 2006). Kernel density estimations of bottom periods of the different foraging groups were computed on SSH and depth using a Gaussian Kernel. These were then overlaid on the vertical thermal structure of different ACC frontal zones following Venables et al. 2012. This allowed us to analyse the penguins' use of the water column with respect to depth and thermal structures relative to frontal zones.

Detailed use of the water column by the penguins while foraging was analysed by considering depth, temperature and temperature gradient during the bottom periods of the dives. Analyses were carried out on data with a resolution of 1 Hz. Contour plots of bottom periods of dives >50 m on depth – temperature gradient and temperature – temperature gradient axes allowed us to evaluate the penguins' use of the water column, and to identify the target of different water masses by the different foraging groups. To identify water masses from the water characteristics targeted by the penguins, we defined 4 water masses based on water temperature (T) and temperature gradient (gradT): thermocline waters ($T \geq 1.5$; $\text{gradT} < 0$), WW in proximity ≤ 25 m of the

thermocline ($T < 1.5$; $\text{gradT} < 0$), WW deeper than 25 m below the thermocline ($T < 1.5$; $\text{gradT} \geq 0$), CDW ($T \geq 1.5$; $\text{gradT} \geq 0$).

Wiggles occurrence and influencing factors

As wiggles are good proxies of prey capture attempts in penguins (Takahashi et al. 2004, Bost et al. 2007, Hanuise et al. 2010), we examined water characteristics where wiggles occurred, with respect to temperature and temperature gradient. We used logistic regression models to quantify relationships between water properties and the occurrence of wiggles for individual as well as for grouped birds. For the regression models, we included temperature and temperature gradient data for dives >50 m depth with a temporal resolution of 1 s, after testing for non-correlation using Pearson's correlation coefficient. The predictor of wiggles occurrence was a combination of the water temperature, the values and the absolute values of the temperature gradient, taking into account the direction of the gradient as well as its intensity. To evaluate model discrimination performances between wiggle presence and absence, we used risk score plots (Royston & Altman 2010). Risk score plots allowed us to graphically compare the densities of the risk score (linear predictor) in the event and no-event group (occurrence and non-occurrence of wiggles). The overlap of the risk score densities determined the discrimination performance of the model: the larger the overlap, the weaker the discrimination.

RESULTS

Identification of different foraging groups

We distinguished 4 foraging groups characterized by differences in breeding stage as well as foraging characteristics (Fig. 2, Tables 1, 2 & 3). The groups were Early Incubation ($n = 4$), Late Incubation ($n = 4$), Brooding I ($n = 3$) and Brooding II ($n = 4$). The PCA of foraging parameters showed the separation of the 4 foraging groups, and allowed the identification of the main variables accounting for the differences (Fig. 2, Table 1). The first principal component was mainly explained by the horizontal and vertical distances travelled. These variables separated the Brooding II from the Incubation groups, with the Brooding I birds spread out in between. Brooding II birds were characterized by the shortest horizontal (Table 2) and

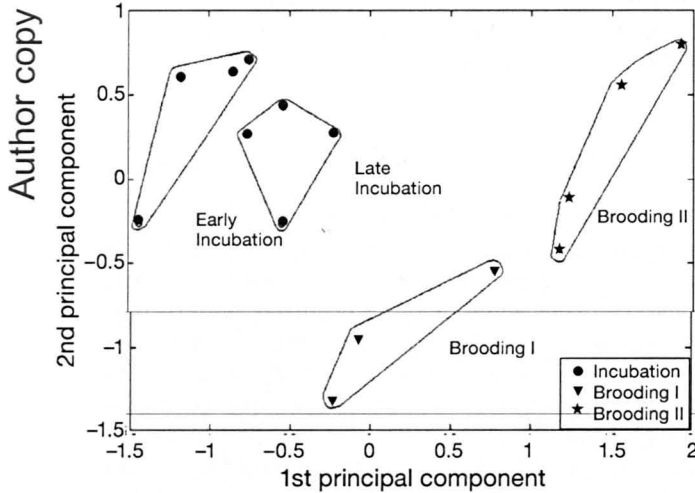


Fig. 2. *Aptenodytes patagonicus*. Principal component analysis of the foraging parameters in the different foraging groups. Component loadings of the variables are listed in Table 1

longest daily vertical (Table 3) distances travelled. The second principal component was mainly loaded with variables of underwater foraging behaviour, separating the Brooding I birds from the Incubation

and Brooding II groups. Brooding I birds were characterized by a dominant bottom phase, high wiggle numbers and a high dive frequency (Table 3). Brooding II birds showed the deepest and longest dives with the shortest bottom periods (Table 3). Broadness index was highest for Brooding I birds and lowest for Brooding II birds (Table 3). A main variable influencing both principal components was the proportion of dive time spent at depths >150 m, separating the Brooding II birds from the Incubation and Brooding I groups (Fig. 2, Table 1).

Trip orientation and foraging areas

All trips were oriented to the north towards the SACCF, AAZ and PF waters, with birds of different breeding stages targeting different foraging areas (Fig. 3) and showing different foraging trip characteristics (Table 2). Early Incubation birds undertook the most extended foraging trips, where increased SSH values indicated PF and Polar Frontal Zone (PFZ) waters. Late Incubation birds targeted areas at the southern edge of the PF and in the AAZ.

Table 2. *Aptenodytes patagonicus*. Trip parameters for individual birds in the different foraging groups (FZC = foraging zone coefficient)

Bird ID	Date of deployment and recovery	Trip duration (d)	Trip length (km)	Max. distance from colony (km)	Min. °S reached	FZC
Early Incubation						
8	23.12.2005–13.01.2006	19.9	2077	642	49.84	3.2
9	28.12.2005–18.01.2006	19.5	2291	522	49.77	4.4
10	30.12.2005–17.01.2006	16.4	1880	520	49.83	3.6
11	30.12.2005–23.01.2006	23.2	2510	537	49.73	4.7
Mean ± SE		19.7 ± 1.4	2190 ± 136	556 ± 29	49.79 ± 0.03	4.0 ± 0.3
Late Incubation						
C5	02.02.2007–20.02.2007	17.3	1585	435	50.77	3.7
C7	02.02.2007–2.02.2007	20.3	1506	409	50.72	3.7
C9	03.02.2007–26.02.2007	23.2	1690	558	51.82	3.0
C10	03.02.2007–17.02.2007	13.4	1150	445	50.40	2.6
Mean ± SE		18.6 ± 2.1	1483 ± 117	462 ± 33	50.93 ± 0.31	3.2 ± 0.3
Brooding I						
H5	09.02.2007–17.02.2007	6.1	610	234	52.55	2.6
H9 (no TDR)	12.02.2007–19.02.2007	6.2	559	227	52.5	2.5
P3	18.02.2007–01.03.2007	9.1	925	317	51.67	3.1
P5	18.02.2007–28.02.2007	7.0	822	346	51.32	2.9
Mean ± SE		7.1 ± 0.7	729 ± 87	281 ± 30	52.01 ± 0.31	2.8 ± 0.1
Brooding II						
H3	09.02.2007–16.02.2007	5.1	491	190	52.98	2.6
H6 (no TDR)	10.02.2007–16.02.2007	5.5	490	159	53.04	3.1
P4	18.02.2007–25.02.2007	6.0	517	163	53.50	3.2
P10	27.02.2007–04.03.2007	4.8	430	112	53.44	3.9
T4	28.02.2007–06.03.2007	5.5	629	247	52.20	2.4
Mean ± SE		5.4 ± 0.2	512 ± 33	174 ± 22	53.03 ± 0.23	3.0 ± 0.3

Table 3. *Aptenodytes patagonicus*. Dive parameters for individual birds in the different foraging groups. KW = Kruskal Wallis test with $p < 0.001$. Dunn's test was performed with $p < 0.05$. The foraging groups show significant differences from others as indicated (all: all other foraging groups; Inc: Early & Late Incubation; BI: Brooding I; BII: Brooding II). VD = vertical distance

Bird ID	Dive depth (m)	Dive duration (s)	Bottom duration (s)	Wiggles per dive	Broadness index	Total VD (km d ⁻¹)	Total dives per day	% of time submerged >150 m
Early Incubation								
8	117.8	246.5	61.6	6.3	0.26	306.5	268.5	2.3
9	130.2	259.0	73.1	8.0	0.28	306.2	209.4	4.7
10	129.0	287.4	92.2	9.1	0.32	266.1	171.0	3.5
11	126.0	260.5	82.6	12.4	0.32	301.8	583.0	3.4
Mean \pm SE	125.7 \pm 2.8	263.3 \pm 8.6	77.4 \pm 6.6	9.0 \pm 1.3	0.30 \pm 0.02	295.1 \pm 9.7	308.0 \pm 93.8	3.5 \pm 0.5
Late Incubation								
C5	134.2	246.8	61.9	10.5	0.25	310.1	412.5	4.1
C7	128.8	260.9	73.3	7.4	0.28	315.1	249.7	4.1
C9	144.1	258.6	54.1	7.1	0.21	297.7	261.3	4.6
C10	122.5	251.4	57.8	5.7	0.23	364.2	361.5	3.1
Mean \pm SE	132.4 \pm 4.6	254.4 \pm 3.3	61.8 \pm 4.1	7.7 \pm 1.0	0.24 \pm 0.02	321.8 \pm 14.6	321.2 \pm 39.4	4.0 \pm 0.3
Brooding I								
H5	145.1	256.0	70.9	9.7	0.28	434.8	327.3	6.4
P3	118.0	249.8	96.2	14.6	0.39	317.1	254.2	2.0
P5	111.3	239.0	81.0	10.4	0.34	333.6	355.4	2.1
Mean \pm SE	124.8 \pm 10.3	248.3 \pm 4.7	82.7 \pm 7.4	11.6 \pm 1.5	0.33 \pm 0.03	361.8 \pm 36.8	312.3 \pm 30.2	3.5 \pm 1.4
Brooding II								
H3	163.8	272.2	57.9	8.8	0.21	432.2	294.2	8.4
P4	201.9	308.4	52.1	6.5	0.17	377.5	249.0	10.8
P10	183.4	288.8	55.5	5.3	0.19	437.6	199.0	12.7
T4	175.8	294.2	68.1	11.4	0.24	424.9	366.4	9.6
Mean \pm SE	181.2 \pm 8.0	290.9 \pm 7.5	58.4 \pm 3.4	8.0 \pm 1.3	0.20 \pm 0.01	418.0 \pm 13.8	277.2 \pm 35.5	10.4 \pm 0.9
KW & Dunn's test	all	BI-BII	BI-BII	BI	BI-BII	Inc-BI&BII	BII	BII

Brooding birds undertook shorter trips into areas south of the PF. Brooding I birds showed highly directed foraging trips into AAZ waters, indicated by low FZC values. Brooding II birds were characterized by less directed foraging trips into the SACCF or its northern boundary.

Vertical habitat use

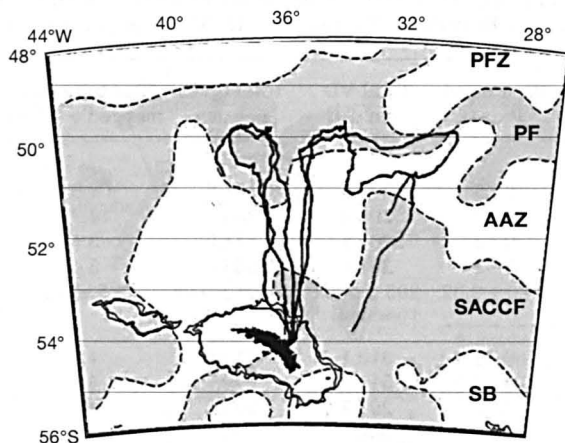
Penguins in the different foraging groups showed differing use of the water column in the various ACC zones (Fig. 4), targeting different depths, water temperatures and temperature gradients during the bottom periods of the dives (Fig. 5). Early Incubation birds foraged in the SACCF, the AAZ, the PF and occasionally in PFZ waters, and explored a broad temperature range of -1 to 6°C , with temperature gradients between 0.5 and -3°C per 50 m. The thermocline and WW appeared to be the most important water masses for bottom times, but there was no clear concentration of bottom times in specific parts of the water column. Late Incubation birds foraged in the

SACCF and in the AAZ until the southern edge of the PF. Bottom periods were directed into waters of -0.5 to 2°C and temperature gradients of up to -4°C per 50 m. Shallow and deep WW were the most targeted water masses. Brooding I birds showed highly focused targeting of shallow waters of strong thermal gradients in the AAZ. Bottom periods were directed into similar conditions to those of Late Incubating birds, but more focused on strong gradients in shallow WW. Brooding II birds concentrated their foraging activity in SACCF waters, where they dived to depths of 100 to 300 m. Bottom periods occurred in a restricted range of temperature and temperature gradient of -0.5 to 2°C and -0.5 to 0.5°C per 50 m, respectively. This indicates the target of deep WW and CDW.

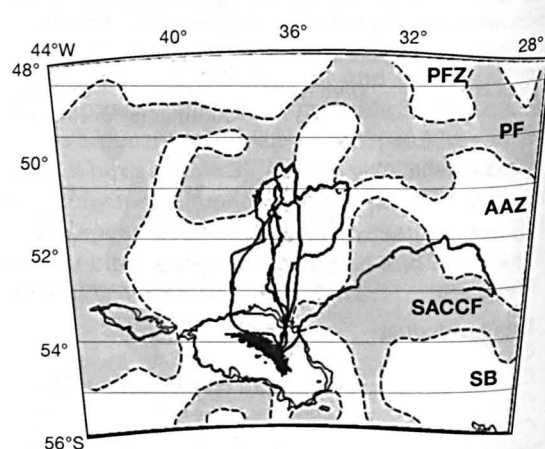
Wiggles occurrence and influencing factors

For incubating birds, the correlations between wiggle occurrence and water properties were generally weak when considered over an entire foraging trip.

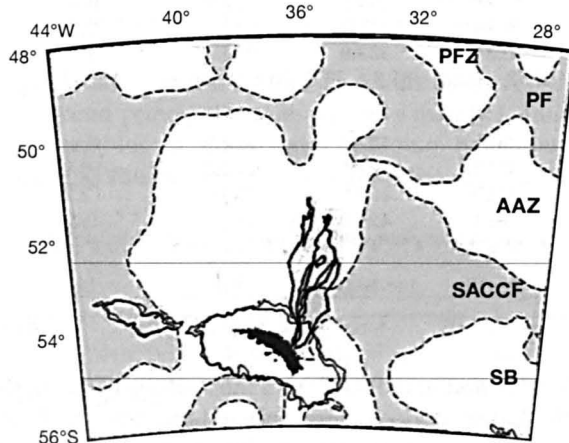
(a) Early Incubation 2005/06 (n = 4)



(b) Late Incubation 2007 (n = 4)



(c) Brooding I 2007 (n = 4)



(d) Brooding II 2007 (n = 5)

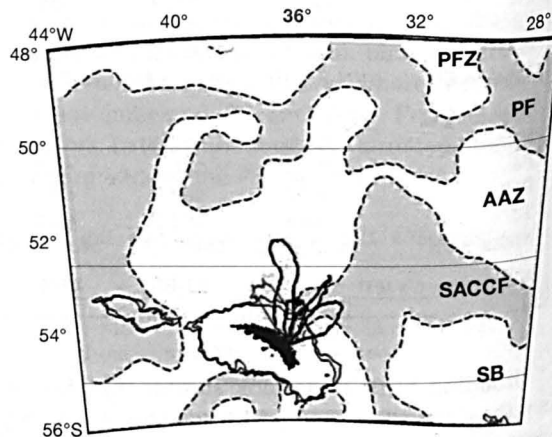


Fig. 3. *Aptenodytes patagonicus*. Tracks of GPS-equipped individuals (a–d) from South Georgia during summer 2005 to 2006 and summer 2007 with the major ACC fronts in the Scotia Sea. Incomplete tracks are due to tag memory limitations or insufficient time at the surface to collect GPS satellite ephemerides. Frontal zones are based on Sea Surface Height (SSH) definitions from Venables et al. (2012). Frontal positions shown on the maps correspond to the mean positions over the trip period of the corresponding foraging group. PFZ: Polar Frontal Zone; PF: Polar Front; AAZ: Antarctic Zone; SACCF: Southern ACC Front; SB: Southern ACC Boundary

In the PFZ, low water temperature appeared to play a more important role for wiggles occurrence than the temperature gradient (Fig. 6 a,b). The logistic regression model showed that wiggle occurrence was greater at negative water temperature gradients for Brooding I birds, and increasing with positive gradient for Brooding II birds (Fig 6c,d). Correlations were stronger for Brooding I than for Brooding II birds. Risk score plots indicated better model discrimination performances for conditions of wiggles absence than of wiggles presence for all birds, and reduced performances for grouped birds compared to the analysis of single birds.

Body mass gain of tracked penguins

Brooding II birds had highest body mass gains per day as well as in relation to horizontal and vertical distances travelled. Brooding I birds showed higher mass gains per day and distances travelled than the Incubation group (Table 4).

DISCUSSION

This is the first study to investigate how a deep diving avian marine predator changes its foraging

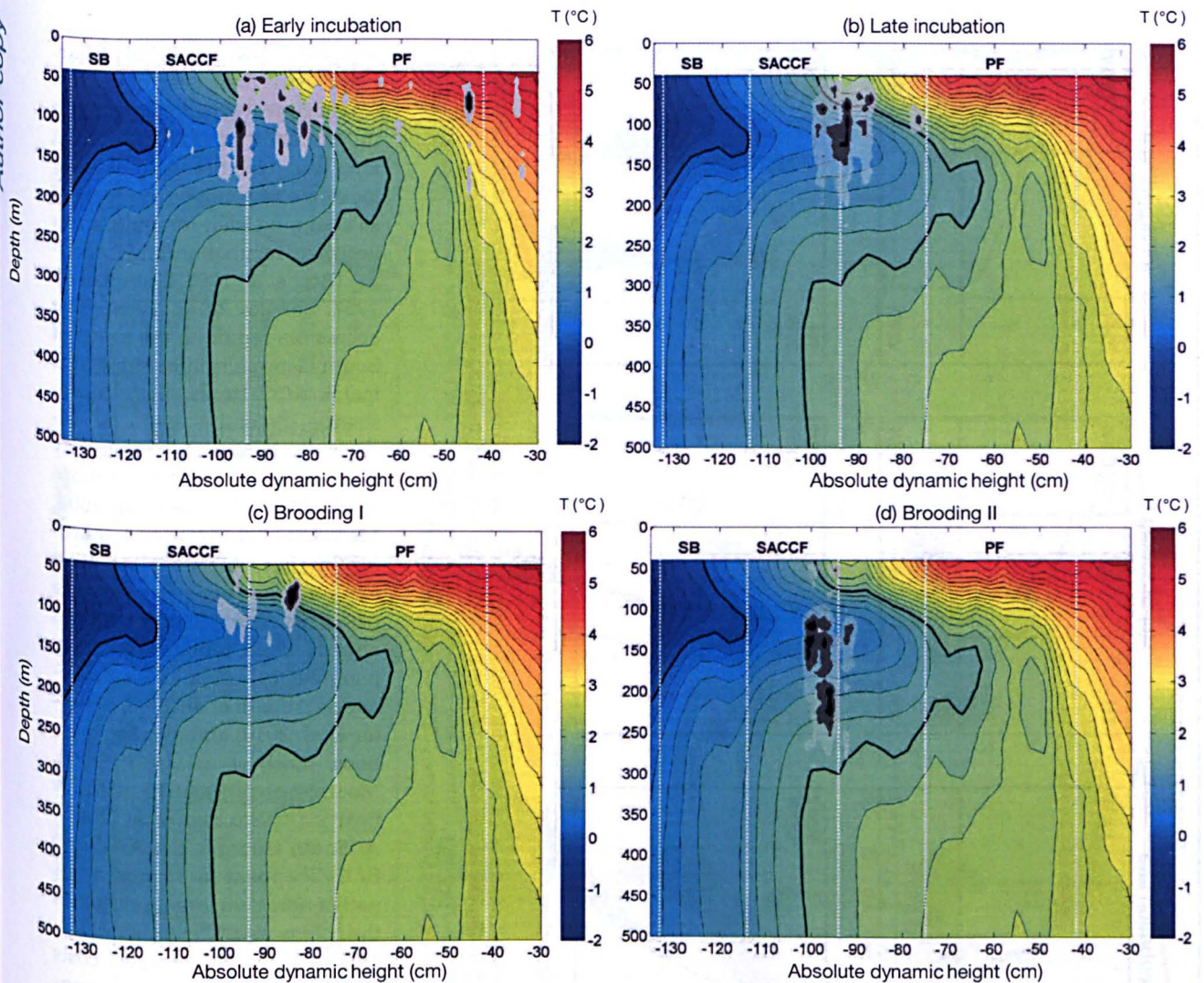


Fig. 4. *Aptenodytes patagonicus*. Kernel densities of bottom times for the different foraging groups (a–d). Density contours encompass 20, 50 and 90 % of the bottom time distributions. Temperature profiles on SSH and depth with ACC front limitations from Venables et al. (2012)

behaviour and habitat use at a fine spatial scale, both vertically and horizontally. The major features of our study are: (1) King penguin foraging behaviour showed different horizontal and vertical patterns over the summer season, presumably in response to changing energetic constraints related to their breeding phase. Foraging trips during incubation extended to the PF, whereas brooding birds foraged exclusively south of the PF in AAZ and SACC waters. (2) Diving behaviour was correlated with the thermal structure of the water column, with the vertical temperature gradient and depth appearing to play important roles for the separation of different vertical foraging niches. (3) Structure in the hydrological environment south of the PF may allow foraging strat-

egy adjustment in relation to changing constraints, and may offer important flexibility for king penguins in the context of environmental variability.

Foraging areas in relation to frontal zones

Areas used for foraging by king penguins changed over the course of the summer season. Birds explored the PF during early incubation and the waters between the PF and the SACC later in the summer season. For seabirds, changes in foraging trip duration at different times of the breeding cycle are known to occur and are thought to be the result of changing time constraints arising from the need to supply the chick

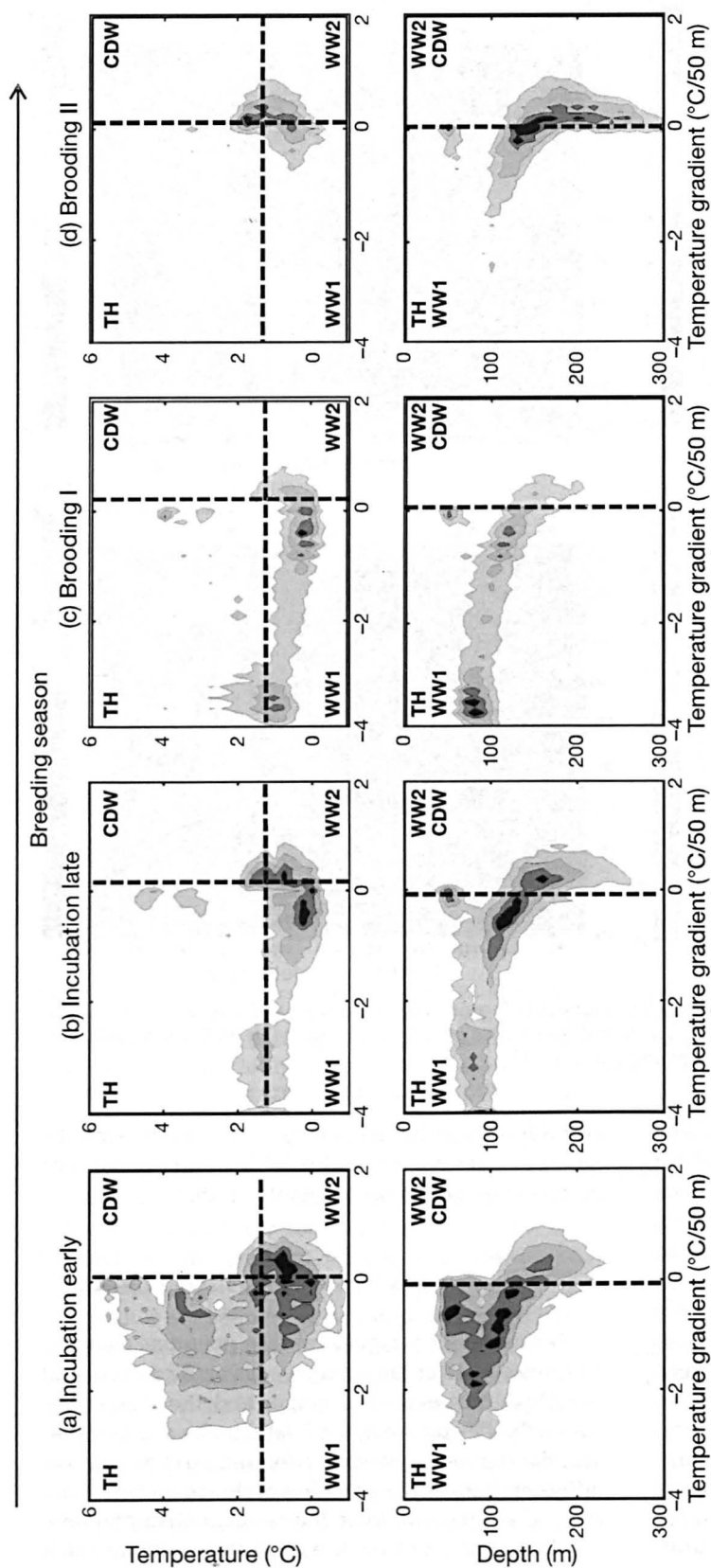


Fig. 5. *Aptenodytes patagonicus*. Environmental niches in the water column targeted by different foraging groups (a–d). Plotted are bottom times of all dives > 50 m on temperature, temperature gradient and depth axes. Contours encompass 10, 25, 50 and 90% of the bottom times of each foraging group. Dotted lines = limits of the water column characteristics used for the definition of the water masses (see Material and Methods). TH = thermocline; WW1 = shallow winter water close to the thermocline; WW2 = deeper winter water; CDW = circumpolar deep water

with food (Bost et al. 1997, Charrassin et al. 1999, Lescroël & Bost 2005). However, in contrast with the situation at South Georgia, king penguins breeding at other locations have not been reported as changing their foraging areas between incubation and brooding (Bost et al. 1997, Guinet et al. 1997, Sokolov et al. 2006). The accessible region to the north of South Georgia is influenced by 2 major ACC fronts, both representing potential areas of increased mesoscale variability (Trathan et al. 1997, 2000, Moore et al. 1999b, Thorpe et al. 2002, Meredith et al. 2003), and, therefore, the possibility of alternative foraging locations for marine predators. The role of the PF has already been reported for king penguins breeding at South Georgia (Trathan et al. 2008, Schaffer et al. 2010) and at other locations (Bost et al. 1997, 2009, Moore et al. 1999a, Charrassin & Bost 2001, Sokolov et al. 2006). At South Georgia, the AAZ and SACCF appear to provide alternative foraging areas closer to the colony. It may allow short foraging trips with low travel costs for birds with high time and energy constraints, as shown by brooding birds, and may, therefore, play a key role for king penguins.

The importance of the SACCF for the Scotia Sea ecosystem has been emphasised in previous studies (Thorpe et al. 2002, 2004, Ward et al. 2002, Murphy et al. 2004;) due to nutrient enrichment resulting in increased phyto- and zooplankton development, possibly resulting in increased myctophid densities associated with these more productive waters. In the AAZ, the meeting of Antarctic waters with warmer PFZ waters as well as the presence of SACCF eddies

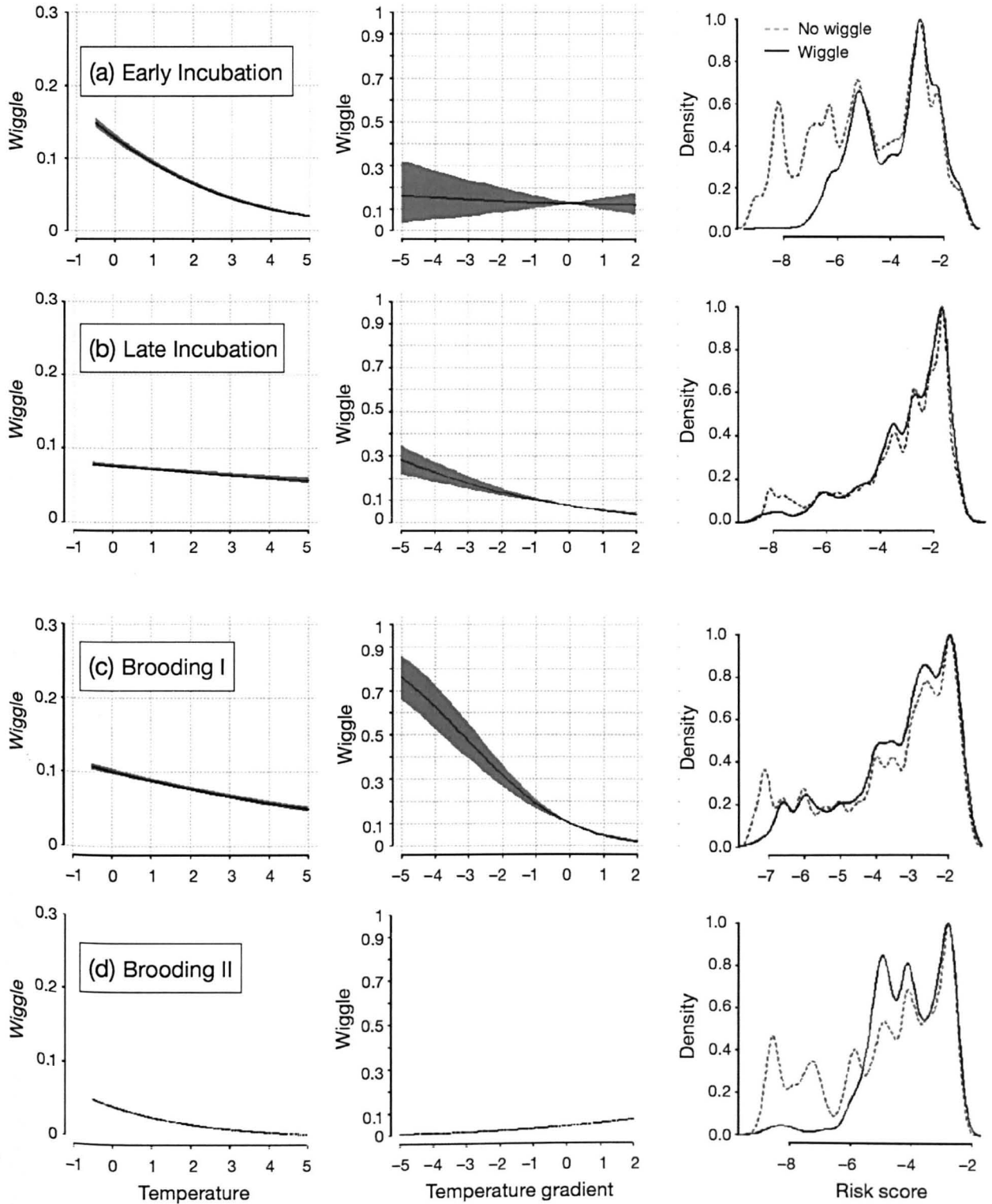


Fig. 6. *Aptenodytes patagonicus*. Wiggles occurrence as a function of water temperature and temperature gradient, and corresponding risk score plots for model discrimination performance. Output of the logistic regression model and risk score plots for (a) 1 Early Incubation and (b) 1 Late Incubation bird. Early Incubation includes data from only within PF and PFZ waters, Late Incubation includes data from the entire trip. (c,d) Model output and risk score plot for (c) 1 Brooding I and (d) 1 Brooding II bird

Table 4. *Aptenodytes patagonicus*. Body mass at start and end of foraging trips as well as total body mass gain per day and per distance travelled for individuals tracked in 2007. HD = horizontal distance; VD = vertical distance

Bird ID	Start weight (kg)	End weight (kg)	Mass gain		
			(kg d ⁻¹)	(kg per 100 km HD)	(kg per 100 km VD)
Late Incubation					
C5	11.4	15.4	0.23	0.25	0.07
C7	11.4	17.0	0.28	0.34	0.09
C9	11.0	14.2	0.14	0.19	0.05
C10	11.8	14.6	0.21	0.24	0.06
Mean ± SE	11.4 ± 0.2	15.3 ± 0.6	0.21 ± 0.03	0.26 ± 0.04	0.07 ± 0.01
Brooding I					
H5	13.8	15.8	0.33	0.33	0.08
H9	13.8	16.9	0.50	0.55	no TDR
P3	12.1	15.1	0.33	0.32	0.10
P5	14.1	17.0	0.42	0.35	0.12
Mean ± SE	13.5 ± 0.5	16.2 ± 0.4	0.39 ± 0.04	0.39 ± 0.06	0.10 ± 0.01
Brooding II					
H3	14.0	16.8	0.55	0.57	0.13
H6	13.0	15.8	0.51	0.57	no TDR
P4	13.8	15.9	0.35	0.41	0.09
P10	12.0	14.5	0.46	0.58	0.10
T4	15.1	17.9	0.58	0.44	0.14
Mean ± SE	13.6 ± 0.5	16.0	0.49 ± 0.04	0.51 ± 0.04	0.12 ± 0.01

(Thorpe et al. 2002, Meredith et al. 2003) may create areas of strong thermal gradients, where myctophids may aggregate (Brandt et al. 1981, Kozlov et al. 1991). Reduced vertical mixing in the AAZ compared to adjacent frontal areas may increase the stability of such thermal structures, therefore favouring associated prey patches (Spear et al. 2001).

King penguins have already been reported to use mesoscale oceanographic features for non-random directed foraging during incubation at South Georgia (Trathan et al. 2008, Scheffer et al. 2010) and at Crozet islands (Cotté et al. 2007). Seasonal changes between foraging areas associated with different larger-scale oceanographic features of elevated mesoscale activity support the hypothesis that king penguin alter their foraging behaviour at different spatial and temporal scales.

Targeted foraging niches in the water column

Our detailed analysis of the time spent at the bottom of the dives, relative to frontal zones and to thermal structures in the water column, allowed us to determine the water masses explored by king penguins over the summer season, and how birds adjust their foraging niches according to breeding constraints.

During December and January, incubating birds foraged in the SACCF, the AAZ and the PF, and

targeted various thermal structures at different depths in the water column. Enhanced vertical mixing in frontal areas (Spear et al. 2001) may lead to increased spatial and temporal variability in thermal structures and associated prey resources. Such dynamic prey distributions may be reflected by the less consistent targeting of specific depth-temperature-gradient patterns of birds foraging in the PF compared to in the AAZ, and only weak correlation of wiggle occurrence with specific temperature gradients.

Late Incubation and Brooding I birds mainly foraged in AAZ waters. Brooding I birds targeted shallow WW in close proximity to the thermocline, and wiggles occurrence was correlated with strong thermal gradients. The importance of sub-thermocline prey aggregations has already been reported for dolphins (Scott & Chivers 2009), tuna (Schaefer et al. 2007) and sunfish (Cartamil & Lowe 2004), and appears to be confirmed for king penguins foraging in the AAZ. Collins et al. (2008, 2012) found that certain myctophid species can be present at shallow depths during daytime in the AAZ in the area to the north of South Georgia. Strong thermal gradients of high stability may represent suitable conditions for stable myctophid aggregations at shallow depths, which have been reported previously associated with warm-core rings in the Gulf Stream (Conte et al. 1986) and in the equatorial Atlantic Ocean, with tuna

also exploiting these aggregations (Marchal & Lebourges 1996, Bard et al. 2002). The diving behaviour of Brooding I birds may indicate the presence of such permanent myctophid layers at shallow depths of 70 to 110 m in the Scotia Sea, even though this has so far only been reported from more temperate regions. However, this hypothesis remains speculative as independent prey data was not available for our study.

Brooding II birds showed significantly deeper dives than the other groups, mainly targeting waters with weak positive temperature gradients at the transition between deep WW and CDW in the SACCF. High body mass gains despite increased dive depths and reduced bottom times suggest increased foraging efficiency in these deep waters. Deep and long dives reported from king penguins at Crozet in autumn (Charrassin et al. 1998, 2002, Halsey et al. 2010) suggest seasonal changes in targeted prey similar to those observed at South Georgia for Brooding II birds. At Crozet, king penguins appear to compensate increased costs for deeper dives in autumn by longer bottom times (Charrassin et al. 2002, Halsey et al. 2010). At South Georgia, king penguins seem to be able to increase foraging efficiency at the bottom of dives. The foraging area targeted by Brooding II birds may provide particular conditions of highly profitable prey resources at great depths, potentially enhanced by the higher nutrient content in areas with the SACCF influx into the Scotia Sea (Ward et al. 2002).

Thermal structure of the water column and foraging

The thermal structure of the water column and depth appeared to play a crucial role for the separation of foraging niches and the expression of different foraging patterns, especially with increasing constraints on the animals. Relative water structures have been suggested to play an important role for vertical movements of other diving predators such as tuna and billfish (Brill et al. 1993, Brill & Lutcavage 2001), sunfish (Cartamil & Lowe 2004), dolphins (Scott & Chivers 2009) and basking sharks (Sims et al. 2005). Foraging tuna and associated tropical seabirds have been reported to be more abundant in non-frontal areas characterized by lower vertical mixing and higher stability of vertical thermal structures (Owen 1981, Spear et al. 2001). King penguins are diving predators that target similar prey; they may, therefore, rely on the same criteria for favourable foraging habitats and show similar affinity with

well structured waters, possibly reflected by targeting distinct niches in non-frontal or border areas by brooding birds. In addition to the importance of frontal zones for Southern Ocean marine predators (Bost et al. 2009), non-frontal or boundary areas with a higher stability of vertical thermal structures may also play a key role for diving predators such as king penguins, especially when constraints limit flexible travel times and behavioural adaptations to dynamic conditions at fronts.

The vertical temperature gradient appeared to be a main factor for foraging niche adjustment and explaining differences in prey pursuit behaviour (wiggle occurrence). Thermal gradients are locations of enhanced biological activity (Thomas & Emery 1988, Lima et al. 2002), resulting in the accumulation of biomass for various trophic levels, ranging from planktonic organisms to mesopelagic fish and ultimately upper trophic level predators. Being one of the most pronounced vertical temperature gradients in the ocean, the thermocline has already been suggested as an important feature for king penguins at Crozet (Charrassin & Bost 2001) as well as for other marine predators foraging in the Southern Ocean (Boyd & Arnborn 1991, Biuw et al. 2007) and in more temperate regions (Cayre & Marsac 1993, Kitagawa et al. 2000, Spear et al. 2001, Weng et al. 2009, Sepulveda et al. 2010). Our study underlines the crucial role of the thermocline for foraging king penguins breeding at South Georgia. It also demonstrates the possibility that king penguins have alternate efficient foraging strategies for exploiting water masses where thermal gradients do not seem to be the main factor governing prey distribution.

Our regression models have revealed some insights into the effect of thermal properties of the water column on king penguins foraging. However, variable regression coefficients between individual birds as well as the prevalence of Brooding I and Brooding II patterns on identical trip departure dates underline the fact that foraging strategies might not only relate to particular environmental conditions. Behavioural plasticity and individual factors (Svanback & Bolnick 2005, Sargeant et al. 2007) such as detailed breeding constraints, fitness and prior experience may also play a role. Lower model performances for wiggle presence than absence may result from the fact that favourable foraging conditions for king penguins are not only determined by the thermal structure of the water column, but may also be influenced by other factors governing prey distribution in a given environment such as stochastic processes and prey behaviour.

King penguins' foraging and environmental variability

Foraging behaviour of king penguins breeding at South Georgia appears to be structured both horizontally and vertically. Penguins targeted different foraging areas depending on their breeding constraints, and adjusted their foraging activity in the water column. So far such strong habitat selection and the presence of alternative foraging niches have not been reported for king penguins from other locations. Patterns described from Crozet suggest changes in foraging characteristics over the summer season similar to those described at South Georgia, with shortening of foraging trips and increasing dive depths. However, penguins in both the incubation and brooding stage target the PF, and foraging patterns appear less diverse than those of king penguins at South Georgia with respect to trip characteristics, diving behaviour and the targeting of distinct niches in the water column (Charrassin et al. 1998, 2002, Charrassin & Bost 2001). This may suggest that alternative foraging areas closer to the colony, as reported from South Georgia, are not available at Crozet.

For king penguins breeding north of the PF (i.e. Crozet, Marion Island), the geographically nearest profitable myctophid aggregations may be found at accessible depths mostly at the PF and its northern edges, as myctophid species targeted by king penguins are known to increase in depth northwards of the PF (S. Fielding pers. comm.). This means that penguins breeding in these locations may depend to a higher degree on the PF. Predicted declines of king penguins due to environmental variability (Barbraud et al. 2008, Le Bohec et al. 2008, Péron et al. 2012) and in case of shifts in the PF may, therefore, only relate to areas where the animals are highly dependent on the PF due to the lack of alternative foraging areas. Such predictions might be of lesser value for king penguins breeding at South Georgia.

King penguins at South Georgia appear to be able to exploit profitable prey resources at the southern edge and south of the PF, either in terms of reduced depth in the AAZ or of increased profitability per catch effort at the bottom in SACCF waters. The area south of the PF may offer an elevated degree of foraging habitat segmentation to king penguins, as other structures than the PF may provide for profitable prey resources at accessible depths. King penguins from Heard Island, also located south of the PF, appear mainly to forage in the area to the east of the island (Moore et al. 1999a, Wienecke & Robertson 2006), a location influenced by the southern branch

of the PF and the Fawn Trough current (Roquet et al. 2009, van Wijk et al. 2010). Foraging in areas outside or at the southern boundaries of the PF, areas characterized by cold water masses, may produce similar patterns to those at South Georgia. However, studies from Heard Island provide no information on diving behaviour in relation to the thermal structure of the water column, or on segregation of foraging areas.

Oceanography at South Georgia is known to be influenced by ENSO (El Niño – Southern Oscillation) and SAM (Southern Annular Mode) as well as more direct atmospheric processes (Trathan & Murphy 2002, Meredith et al. 2008). However, different time lags between these events and the response in oceanography at South Georgia occur (Meredith et al. 2008), as well as temporal variation in the connections within the Scotia Sea ecosystem (Murphy et al. 2007). Our study includes reports of only one season per foraging group. Therefore, it remains open as to whether the patterns observed are a constant element in the foraging strategy of king penguins breeding at South Georgia, or whether they are a response to particular conditions during our study years. Nevertheless, the oceanographic patterns observed during our study appear to be consistent with general patterns described in the area to the north of South Georgia (Trathan et al. 1997, 2000, Thorpe et al. 2002, Meredith et al. 2003, Brandon et al. 2004). Also, the temporal and spatial scales of the oceanographic features considered exceed the duration of the tracked foraging trips. Low sample sizes of the different foraging groups may raise questions about conclusions on general behavioural patterns at a population level. Even so, the foraging patterns observed during brooding indicate the presence of optional foraging niches close to shore at South Georgia, allowing foraging of potentially increased efficiency, at least in some years. This might also play a key role in potential responses of king penguins to environmental changes (Forcada & Trathan 2009), as optional foraging niches may allow them to better adjust foraging behaviour in response to the prevailing oceanographic conditions.

Acknowledgements. This work is a contribution to the BAS Ecosystems programme, jointly funded by BAS and CNRS. The authors are grateful to C. Bishop for the provision of waterproof housings for the NavSys Track-Tag devices and to H. Venables and S. Thorpe for advice on the oceanography around South Georgia. M. Authier provided help with data analysis, and constructive comments that improved the manuscript. We thank J. Edmonston for help with data organisation and preparation, and C. Thomas for assistance with data collection in the field. Four anonymous reviewers provided helpful comments that greatly improved the manuscript.

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Editorial responsibility: Matthias Seaman,
Oldendorf/Luhe, Germany

Submitted: June 27, 2011; Accepted: June 18, 2012
Proofs received from author(s): September 17, 2012

Foraging habitat and performances of King penguins *Aptenodytes patagonicus* Miller, 1778 at Kerguelen islands in relation to climatic variability

by

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ABSTRACT. - Understanding how climate change affects the foraging ecology of key marine predators is an important issue in the study of Southern Ocean food webs. Since 1998, we have conducted a long term research program on the foraging ecology of a top-diving predator, the King penguin *Aptenodytes patagonicus*, simultaneously at Kerguelen and Crozet Islands with the support of the IPEV (Institut Polaire Français). King penguin is one of the most important predatory birds at Kerguelen. In summer, they forage preferentially along large-scale physical features and use the three dimensions of hydrographic features to feed on myctophid fishes (the penguins' main prey and a major prey species in the Southern Ocean). Primarily, this study aims to evaluate how the change in foraging parameters and success of penguins reflect the impact of oceanographic conditions on key food webs in the polar frontal zone. Each summer, breeding (incubation and brooding) penguins from the Ratmanoff colony (Coubet Peninsula, Kerguelen; 100 000 pairs) are instrumented with Argos transmitters or GPS with time-temperature-depth recorders. Here we provide a first modelling approach to the King penguin's foraging habitat during summer from static variables (bathymetry), dynamic variables (SSHt, SST, Chlorophyll) and their related trends (gradients). In addition, trawl data on the distribution of myctophid fishes have been integrated. The most important factors explaining penguin foraging location are the SSHt, the bathymetry gradient and the SST. Results of interannual change in penguins at-sea trajectories, diving behaviour, foraging success and effort are discussed according to the interannual changes in the hydrographic structure in the Kerguelen region.

RÉSUMÉ. - Habitat d'alimentation du manchot royal (*Aptenodytes patagonicus*) à Kerguelen.

Comprendre comment les changements climatiques vont affecter les prédateurs supérieurs marins de l'océan Austral et les chaînes trophiques dont ils dépendent est d'un intérêt majeur. Depuis 1998, nous menons un programme de recherche à long terme sur les stratégies alimentaires d'un prédateur marin plongeur, le manchot royal *Aptenodytes patagonicus* aux îles Kerguelen et Crozet, avec le support de l'IPEV (Institut Polaire Français). Le manchot royal est un des prédateurs marins les plus importants de Kerguelen, en termes de biomasse consommante. En été, les manchots royaux se nourrissent préférentiellement de poissons de la famille des myctophidés, un groupe clé des chaînes trophiques de l'océan Austral. Ils recherchent leurs proies préférentiellement au niveau de caractéristiques physiques à grande échelle et utilisent les 3 dimensions de la structure hydrologique. Un des objectifs de notre étude est d'évaluer comment les changements dans l'écologie alimentaire des manchots vont refléter l'impact des conditions océanographiques à l'échelle locale et à grande échelle, sur les chaînes alimentaires dont ils dépendent. A cette fin, des manchots partant en mer pour se nourrir sont équipés de balises Argos, GPS ou enregistreurs de plongée / température de l'eau, durant chaque été austral. A Kerguelen, la colonie étudiée est située à Ratmanoff, sur la façade est de la péninsule Coubet (100 000 couples). Nous présentons ici la première approche de modélisation de l'habitat alimentaire en mer des manchots, à partir de l'analyse des variables statiques (bathymétrie) et dynamiques (température et hauteur de l'eau et leurs gradients, chlorophylle et gradients associés). Les données des pêches scientifiques existantes sur la distribution des myctophidés ont été intégrées. Les facteurs explicatifs les plus importants vis-à-vis de la distribution en mer des manchots sont les anomalies des hauteurs d'eau et les gradients associés, la température de l'eau et le gradient de bathymétrie. Les résultats des changements d'année en année des trajectoires en mer des manchots, du comportement de plongée et de leur effort de pêche sont discutés en perspectives des changements hydrologiques affectant l'écosystème de Kerguelen.

Key words. - Climate variability - Top-predators - Penguins - Foraging - Habitat modelling - Kerguelen.

The Southern Ocean is one of the marine areas most susceptible to climate change (Trathan *et al.*, 2007). The detection and quantification of the impact of the climatic vari-

ability on the biodiversity of this ocean and its food webs have been given high international priority because it still accommodates the planet's largest unexploited animal bio-

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mass (Atkinson *et al.*, 2004). However, the links between the physical features of the Southern Ocean, biological productivity and the distribution and abundance of zooplanktonic and nektonic prey remain poorly understood.

Considering these difficulties, it has been proposed that the foraging behaviour of tagged predators could be used as bio-indicators of the availability of underlying resource distribution (Wilson *et al.*, 1994; Bost *et al.*, 1997; Wilson *et al.*, 2002; Austin *et al.*, 2006). Many marine birds from these areas are wide-ranging predators, highly mobile, and dependent on secondary and tertiary productivities. At sea, they strive to forage efficiently to maximize their chances of reproductive success (Lescroël *et al.*, 2010).

Most research efforts concerning pelagic resources in the Southern Oceans have been devoted to the change in the status of krill stocks (Atkinson *et al.*, 2004). However, the mesopelagic fishes (Family Myctophidae) are also an important biological resource, in which biomass is estimated at $200\text{--}400 \times 10^6$ tons (e.g., Lubimova *et al.*, 1987; Pakhomov *et al.*, 1994). Additionally the distribution of these small schooling fish is closely related to the thermal structure of the water mass (Torres and Somero, 1988). Myctophids are difficult to sample using traditional techniques because of their patchy distribution and mobility (Duhamel 1998). Diving top predators such as King penguins *Aptenodytes patagonicus* Miller 1778 are good candidates to investigate the inter-annual and long-term change in myctophid distribution. King penguins are one of the most important avian consumers of the Southern Ocean (Guinet *et al.*, 1996). It is also one of the most specialized seabirds in terms of diet, relying almost exclusively on myctophid fishes during the summer (Cherel and

Ridoux, 1992). They are deep divers and pelagic foragers able to routinely dive deeper than 250 m and to forage up to 400 km from their colonies (Bost *et al.*, 2002).

Since 1998, we have conducted a long term research program on the King penguin foraging ecology at Kerguelen Islands. The aim of the project is to evaluate how the changes in foraging parameters and success of an avian top predator can reflect and predict change in the availability of myctophids in one of the most productive ecosystem of the Polar Frontal Zone, the Kerguelen archipelago.

Here we provide a first modelling approach of the King penguins foraging habitat during summer at Kerguelen. The habitat model was developed to explain and predict spatial distribution of foraging effort within the penguins' available geographic range. This was carried out from the analysis of penguins foraging activity (*via* a bio-logging approach) over four years (1999-2002) concurrently with both datasets describing physical and biological oceanography.

MATERIALS AND METHODS

The project relied on the long-term monitoring of penguins movements at sea and foraging effort during the breeding season depending on oceanographic conditions. Each summer, breeding (incubation and brooding) penguins from the Ratmanoff colony (Courbet Peninsula, 100 000 pairs) are instrumented with Argos transmitters or Fast-loc GPS (Sirtrack: Havelock North, NZ), and Time-Temperature-Depth recorders (MK7 to MK9, Wildlife Computers: Redmond, WA, USA).

We used the spatial distribution of dives to determine the at-sea distribution of the foraging habitat. Only dives deeper than 50 m were used as most of the feeding activity occurs beyond that depth (Charrassin *et al.*, 2002a). This corresponded to a total of 27 271 foraging dives recorded on 27 birds from 1998 to 2002. A grid of 0.2° cell size was designed over the Kerguelen shelf and in each cell the number of dive was recorded. Only cells where at least three different individuals had dived were kept ($n = 107$, 54% of the dives; Fig. 1). The number of foraging dives was then log-transformed. Finally the number of dives per grid cell was modelled according to three types of environmental components: the spatial, physical and biological component. Dynamic oceanographic variables (surface height, sea surface temperature, chlorophyll concentration) were extracted for each grid cell from both sources of oceanographic information (model and satellite), whereas static variables such as bathymetry was obtained from the National Oceanic and Atmospheric Administration's (NOAA) ETOPO dataset, and their gradient (in terms of slope between each cell) computed.

In addition, myctophid presence-absence (distribution trawls data on the Kerguelen shelf from the *Ichtyoker* data-

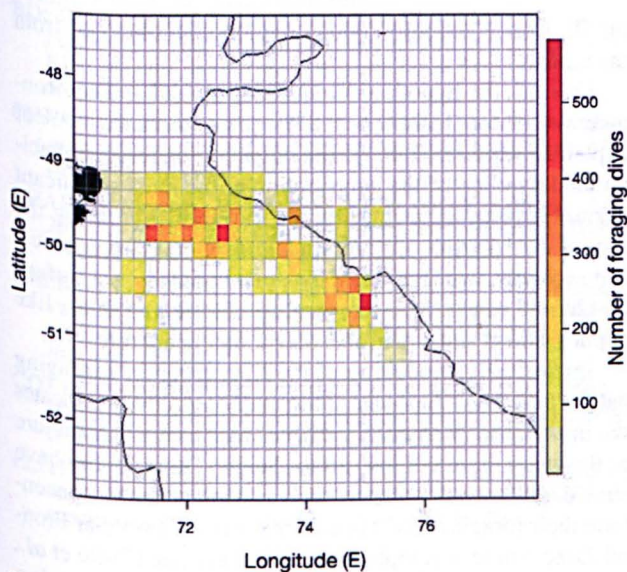


Figure 1. - Foraging dives distribution of King penguins satellite-tracked from Ratmanoff Colony, East of Kerguelen Islands ($n = 4$ years, 1998-2002, 27 271 dives, $n = 27$ birds).

base, 1998-2000) was modelled according to the four previous environmental variables and their gradient. A model was performed using Random Forests, a machine-learning method combining three models trained on different bootstrap replicate sample of the data (Elith and Graham, 2009). We used data from night trawls at depths ranging from the surface to 100 m ($n=73$ trawls), performed from January to March (Duhamel 1998; Guinet *et al.*, 2001). The performance and evaluation of the model was evaluated using a Leave-one-out cross-validation.

The variable testing procedure for assessing penguin foraging habitat was based on the test of the main variables and their possible combinations, which provided seven hypoth-

eses (Tab. I). A bootstrap procedure (Potts and Elith, 2006) was performed to evaluate the performance of each modelling hypothesis (10 000 simulations).

RESULTS AND DISCUSSION

At Kerguelen, King penguins are distributed in an area dominated by complex interactions between the proximity of the polar front, bathymetry and current advection. They forage at a mean distance of 300 km off the colony and target mainly waters along the shelf break that are associated with the Polar Front. We used the most important phys-

ical and biological variables and parameters likely to determine the penguin's foraging distribution.

The three main influencing variables follow. First, the spatial distribution of dives, which are strongly autocorrelated at different scales. To determine the corresponding spatial scales, a principal coordinate analysis of neighbour matrices (PCNM) was performed (Dray *et al.*, 2006) (Tab. I). Six spatial scales were retained in the analysis (Fig. 2). Second, the environmental variables, which includes the physical (static: bathymetry; dynamic: SST, sea surface height anomaly) and biological variables (chloro-

phyll). Lastly, the prey fields (myctophids) obtained from the model.

Overall, the hypothesis combining spatial and environmental variables had the best average performance (45% of explained variance, Tab. I). The output of the foraging habitat model indicated the contribution of the most significant variables (Fig. 2), primarily, the variable combining the spatial distribution of dives and environmental variables; and secondly, two significant dynamic variables, sea surface height and sea surface temperature. Static variables, like depth gradient and depth, also play a significant role.

Intrinsically, modelling of the King penguin's foraging habitat based on a four-year study of diving activity indicates the importance of physical variables such as the temperature of the water mass and sea surface height. Other studies have shown how oceanic foragers such as King penguins concentrate their foraging effort in colder waters of the Polar Frontal Zone where myctophids tend to aggregate (Cotté *et al.*, 2007; Bost *et al.*, 1997). In the Crozet sector, the foraging activity occurs within mesoscale frontal zones and strong currents, both associated with eddies at the Polar Front (Cotté

Table I. - Tests of the hypothesis predicting the distribution of the king penguin foraging habitat at Kerguelen Islands (RMSE: Root Means Square Error; AVE: Average Error). The letters m and b correspond to the coefficients of a linear regression between the observed and predicted values: observed = $m \times \text{predicted} + b$. The hypothesis with the best performance is indicated in bold.

Hypothesis	Pearson	Spearman	m	b	RMSE	AVE	Variance explained
"Space"	0.652	0.631	1.232	-0.467	0.259	0.000	27.9%
"Physical Environment"	0.667	0.487	1.502	0.025	0.236	0.004	28.1%
"Prey"	0.481	0.142	1.017	-1.326	0.278	-0.001	17.3%
"Space + Environment"	0.787	0.703	1.217	-0.448	0.203	0.004	45.1%
"Space + Prey"	0.741	0.647	1.311	-0.635	0.222	0.001	39.3%
"Environment + Prey"	0.665	0.487	1.515	-0.044	0.238	0.006	29.1%
"Space + environment + prey"	0.784	0.690	1.251	-0.518	0.203	0.004	43.7%

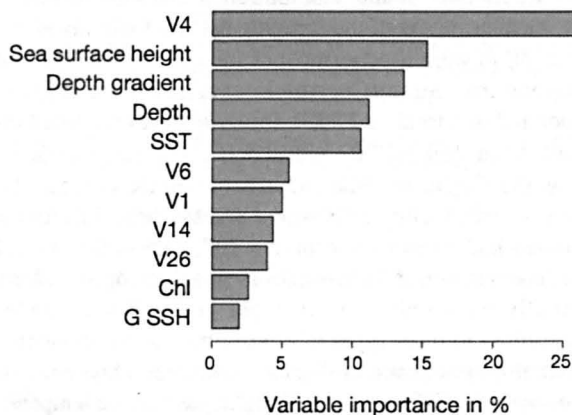


Figure 2. - Output of the foraging habitat model showing the most important variables (Hypothesis "Space + environment"). V1: large scale distribution of dives (Kerguelen North and South); V4: mesoscale distribution of dives (range 100 km, including the 2 areas of highest diving activity); V6: mesoscale distribution of dives (range 76 km, limit of the studied area); V14: mesoscale distribution of dives (range 52 km, restricted diving zones, Kerguelen North); V26: mesoscale distribution of dives (range 47 km); V34: fine scale distribution of dives (range < 10 km) [not shown].

et al., 2007). However, this study also confirms the role of the extensive Kerguelen plateau as a major physical variable driving the foraging behaviour of such pelagic forager (Charrassin et al., 2002b). Climate change scenario predicts a major southern shift of the polar front during this century (Solomon et al., 2007). In the future, warmer surface waters and increased frequency of mesoscale warm anomalies may alter the myctophid distribution and the foraging success of the penguins and other top-diving predators. Next steps will be to model the foraging habitat/prey distribution in distinct climatic scenarios and to evaluate the foraging responses of the penguins in different modelled foraging habitats by using Behaviour Based Models (Grimm and Railsback, 2005).

Acknowledgements. - The project is supported financially and logistically by the Institut Français pour la Recherche et la Technologie Polaires (IPEV) (prog. 394), Terres Australes et Antarctiques Françaises (TAAF) and the ANR 07 Biodiv 'Glides'. We would like to thank all the volunteers, colleagues and those involved in the research of top predators ecology.

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